

Biological and reproductive parameters of *Helicoverpa armigera* and *Helicoverpa zea* reared on artificial diet in Argentina

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Abstract

Helicoverpa armigera and *H. zea* (Lepidoptera Noctuidae) are genetically and physiologically closely related species that have mating compatibility under laboratory conditions. Considering the presence of *H. armigera* in Argentina, the lack information about its biology and evolutionary relationship with *H. zea*, the aim of this study was to compare biological, reproductive, population parameters and biotic potential (BP) of both species under controlled conditions. Egg and larva duration showed significant differences, being in both cases the longest duration in *H. zea*. Pre-oviposition, oviposition, and post-oviposition duration, and fertility presented significant differences. The only population parameter that did not differ between *H. armigera* (96.95) and *H. zea* (104.78) was the net reproductive rate (R_0). The maximum rate of population growth occurred in the day 34 and 46 for *H. armigera* and *H. zea* respectively. Biotic potential value indicated that each female of *H. armigera* and *H. zea* can produce more than 36 quintillion and 454 trillion descendants per year respectively. These analyses determined that *H. armigera* and *H. zea* have the potential to increase quickly their populations under controlled conditions. The results obtained provide additional information to plan and implement strategies for the integrated management of these species with emphasis in *H. armigera* in Argentina.

Key words: Heliothinae complex, growth, development, life table, biotic potential.

Introduction

The Heliothinae complex (Lepidoptera Noctuidae) of agricultural importance in Argentina encompasses *Helicoverpa gelatopoeon* (Dyar), *Helicoverpa zea* (Boddie), *Chloridea virescens* (F.), and *Helicoverpa armigera* (Hubner). Until 2012, *H. armigera*, the old world bollworm, had not been reported in the Americas. However, this species began to be detected from 2013 in different countries of the Americas (Brazil, Argentina, Uruguay, Paraguay, Bolivia, Uruguay, Puerto Rico, USA) (Czepak *et al.*, 2013; Specht *et al.*, 2013; Tay *et al.*, 2013; Mastrangelo *et al.*, 2014; Murúa *et al.*, 2014b; Smith, 2014; El-Lissy, 2015; Hayden and Brambila, 2015; Arnemann *et al.*, 2016). The wide geographic distribution and polyphagia of *H. armigera* promoted its simultaneous occurrence with other endemic Heliothinae species of the Americas, which previously evolved allopatrically (Leite *et al.*, 2014; Murúa *et al.*, 2016).

Considering the phylogenetic relationships within the genus *Helicoverpa*, there is a phylogenetic proximity between *H. zea* and *H. armigera* (Mitter *et al.*, 1993; Laster and Hardee, 1995; Laster and Sheng, 1995; Behere *et al.*, 2007; Jones *et al.*, 2019). *H. zea* is morphologically similar to *H. armigera*, and these two species diverged around 1.5 million years ago (Behere *et al.*, 2007). Thus both species are considered sibling species due to high morphological similarity, genetic proximity, emission the same pheromone compounds, but in different concentrations and the capacity of interspecific crosses between

both species under natural and controlled environmental conditions (Mitter *et al.*, 1993; Laster and Hardee, 1995; Laster and Sheng, 1995; Pogue, 2004; El-Sayed, 2020; Cho *et al.*, 2008; Tay *et al.*, 2013; Anderson *et al.*, 2018; Cordeiro *et al.*, 2020).

H. armigera is native to the Old World (Asia, Europe, Africa, and Australasia) and is one the most important pests worldwide. It is a polyphagous agricultural pest and was reported in more than 180 cultivated and wild plants, encompassing about 45 families. Its preferred hosts are from the following families: Asteraceae [*Helianthus annuus* (sunflower), *Cynara cardunculus* (artichoke), *Chrysanthemum* spp.], Poaceae [*Zea mays* (maize), *Triticum aestivum* (wheat), *Oryza sativa* (rice), *Sorghum* spp., *Saccharum officinarum* (sugarcane)], Fabaceae [*Glycine max* (soybean), *Cicer arietinum* (chickpea), *Pisum* spp. (peas), *Phaseolus* spp. (beans), and forage legumes], Malvaceae [*Gossypium hirsutum* (cotton), *Abelmoschus esculentus* (okra), *Theobroma cacao* (cacao)], and Solanaceae [*Solanum lycopersicum* (tomato), *Solanum tuberosum* (potato), *Capsicum annuum* (bell pepper), *Nicotiana tabacum* (tobacco)] (Reed, 1965; Fitt, 1989; Czepak *et al.*, 2013; Tay *et al.*, 2013; Cunningham and Zalucki, 2014; Burgio *et al.*, 2020; Cordeiro *et al.*, 2020; USDA, 2020).

H. zea, the corn earworm, has a wide distribution in the Americas. It is located from Canada to the south of Argentina. In South America, its populations are endemic in Argentina, Brazil, Paraguay, Chile and Uruguay (Pastana, 2004). This species is polyphagous, and its larvae

have been identified affecting leaves and fruits in more than 100 species, such as maize, sorghum, cotton, tobacco, soybean, tomato, lettuce, among others (King and Coleman, 1989; Capinera, 2000). Among cited host plants, the adults of *H. zea* show a marked preference for maize; because of this, it is considered a major pest of this crop (King and Coleman, 1989; Capinera, 2000; Vincini and Alvarez Castillo, 2009).

The presence of *H. armigera* in Argentina (Murúa *et al.*, 2014b) has led to the need to initiate studies on different biological aspects with Argentinean populations. Although studies of molecular identification, population fluctuation, and geographical distribution of this species were made (Arneodo *et al.*, 2015; Murúa *et al.* 2014a, 2016), no studies have been performed to investigate different biological aspects under controlled environmental conditions and the comparison with *H. zea*, its close related specie. On the other hand, few studies of *H. zea* performance through field and laboratory studies were made in Argentina (Iannone and Leiva, 1995; Navarro *et al.*, 2009; Vincini and Alvarez Castillo, 2009; Tulli *et al.*, 2012a; 2012b; 2012c, 2015) and, as mentioned, no studies have been made comparing different biological aspects between this specie with *H. armigera*.

In Brazil, high infestations of *H. armigera* were observed and recorded in different locations and crops (Czepak *et al.*, 2013; Specht *et al.*, 2013; Tay *et al.*, 2013; Bueno *et al.*, 2014). However *H. armigera* was confused with native species (*C. virescens*, *H. gelatopoeon* and *H. zea*) and its identification and notification occurred (Sosa-Gómez *et al.*, 2016) only when its populations became very high. If this occurs in Argentina, could lead to many speculations about the damage of these two species in the field. Therefore, it is important to compare biological, reproductive, population parameters, biotic potential (BP) and, survival under controlled environmental conditions between both species to understand their population dynamics in the field (Cunningham and Zalucki, 2014; Barbosa *et al.*, 2016).

On the other hand, life table is an appropriate tool to study the dynamics and management of pest populations, because this tool can provide very important demographic parameters which include analysing population stability and structure, estimating extinction probabilities, predicting life history evolution, predicting outbreak in pest species, and examining the dynamics of colonizing or invading species (Deb and Bharpoda, 2016).

Considering the presence of *H. armigera* in Argentina, the lack information about its biology, life table, population parameters, BP and evolutionary relationship with *H. zea*, the aim of this study was to compare biological, reproductive and population parameters between *H. armigera* and *H. zea* from Argentina reared on artificial diet at controlled environmental conditions. Such information can aid in predicting the ability of these species to successfully exploit agroecosystems and provide additional information to plan and implement strategies to control of these species in Argentina. In addition, this information on biological parameters will be useful for comparative purposes in possible hybridization scenarios between both species.

Materials and methods

Insect collections

Adults of *H. armigera* were collected from August to October 2014 with a light trap in a commercial chickpea field. Moths were identified according Pogue (2004) and Navarro *et al.* (2009). All adults were placed in cylindrical cages with metal mesh (40 cm high and 20 cm diameter). Larvae of *H. zea* were collected in Jan 2015 in a commercial maize field. A minimum of 300 larvae (instars 2-5) were gathered and placed individually in glass tubes (12 cm high and 1.5 cm diameter) with pieces of artificial diet until adult emergence.

For both species, adults and larvae were collected in San Agustín county (26°50'21"S, 64°51'32"W) (Tucumán Province, Argentina). Collected adults and larvae were taken to the laboratory and placed in breeding chambers under controlled environmental conditions (27 ± 2 °C, 70-75% relative humidity, 14:10 L:D photoperiod). Sampled insects from each of these species were deposited as voucher specimens in the insect collection of the Sección Zoología Agrícola, Estación Experimental Agroindustrial Obispo Colombres, Tucumán, Argentina.

Insect rearing

Adults collected of *H. armigera* and adults from reared larvae collected of *H. zea* in the commercial chickpea and maize field respectively were arranged in four cylindrical oviposition cages (40 cm high and 20 cm diameter) lined with polyethylene bags, with approximately 25 females and 25 males per cage. For aeration, both ends of the cage were covered with a nylon cloth. The nylon of the upper end of the cage was used as the oviposition substrate and was replaced every day. Each species was maintained in the same chamber under identically controlled environmental conditions at 27 ± 2 °C, 70-75% RH and a photoperiod of 14:10 L:D.

The food for adults was provided via a cotton plug saturated with a mixture of honey and water (1:1 volume: volume) which was replaced every day. Cages were checked daily for oviposition and adult mortality. When adults of both species died, they were examined using male genitalia to confirm the species according to Pogue (2004).

Pieces of nylon with eggs were cut and put into plastic containers of 1000 ml. Once emerged, neonate larvae were placed individually in glass tubes with artificial larval diet that included chickpea flour (Grandiet[®], Buenos Aires, Argentina), wheat germ (Grandiet[®], Buenos Aires, Argentina), brewer's yeast (Calsa[®], Tucumán, Argentina), Agar-agar (TodoDroga[®], Córdoba, Argentina), vitamin C (Anedra[®], Buenos Aires, Argentina), sorbic acid (Anedra[®], Buenos Aires, Argentina), sodium benzoate (TodoDroga[®], Córdoba, Argentina), vitamin supplement amino acids (Ruminal[®], Buenos Aires, Argentina) and methylparaben (Todo Droga[®], Córdoba, Argentina) (Murúa *et al.*, 2003). Artificial diet was replaced every two-three days. As larvae pupated, pupae were sexed and placed in containers with moistened filter paper until adult emergence. Adults were used to initiate a new generation. Both species were reared in artificial diet, according to the methodology described by Herrero *et al.*,

(2017; 2018). After establishing a colony for each population, larvae from the 2nd to the 4th generation were used for studies of biology and population parameters.

Biological and reproductive parameters

From the experimental colony of *H. armigera* and *H. zea*, 218 and 110 eggs respectively were randomly selected to analyse development and survivorship of the different stages (egg, larvae instars, pupa and adult) and the resulting sex ratio.

Each egg was individualized and monitored separately from each other until pupal stage. From the adults obtained, 42 females and 38 males and 21 females and 20 males of *H. armigera* and *H. zea* respectively were used 37 (*H. armigera*) and 20 (*H. zea*) couples to determine longevity and reproductive parameters. One virgin female and one virgin male (less than 24 h old) were paired in cylindrical oviposition cages similar to those described above. Moths were maintained in this cage, with mortality and oviposition recorded daily until the female died. Dead females were dissected to assess the number of spermatophores present in their reproductive tract immediately after death to determine whether mating had occurred (Perfectti, 2002; Rhainds, 2010). Preoviposition, oviposition and postoviposition period duration (days that the female survives after carrying out last oviposition), total fecundity (number of eggs deposited by a female during her entire life period), egg duration, total fertility (percentage of eggs hatching), and adult longevity were recorded.

Life tables

Age-specific survival (l_x , percentage of females alive at specific age x) and age-specific fecundity (m_x , number of female offspring produced by females at age x) were determined for each day (x) that the females were alive.

These parameters were used to construct life tables and to estimate population parameters of *H. armigera* and *H. zea*. The methodologies described by Rabinovich (1978), Sedlacek *et al.* (1986), Carey (1993; 1995) and Bellows and Van Driesche (1999) were used. From age-specific survival (l_x) and fecundity (m_x) schedules, the following population parameters were computed: the net reproductive rate, i.e. the number of times that a population increases during the life cycle [$R_0 = \sum(l_x m_x)$]; time interval between generations [$T = \sum(x l_x m_x) / \sum(l_x m_x)$]; intrinsic rate of increase ($r = \ln R_0 / T$); population doubling time ($DT = \ln 2 / r$) and finite rate of increase ($\lambda = e^r$), which corresponds to the number of individuals which will produce females, added to the population per female/day. The survival analysis was performed following the methodology described by Rabinovich (1978) and Carey (1993; 1995).

Biotic potential

After establishing the biological parameters, the biotic potential (the maximum reproductive capacity of an organism under ideal environmental conditions) was calculated. According to Silveira Neto *et al.* (1976), Montezano *et al.* (2013), Silva *et al.* (2017), Herrero *et al.* (2018) and Specht *et al.* (2019), BP was calculated using this equation: $BP = (sr*d)^n - ER$, where: (sr) sex ratio is number of females divided by number of females plus

number of males; (d) viable individuals per female; (n) number of generations per year or 365 days divided by the total lifespan; and (ER) environmental resistance, assuming no ER took place while the insects were reared in the laboratory.

Data analysis

The data obtained were tested for normality using the Shapiro-Wilk test (Shapiro and Wilk, 1965). The data regarding *H. armigera* and *H. zea* obtained about biological, reproductive and population parameters that did not show normal distribution or homogeneity of variance were subjected to a square root transformation [$\sqrt{(X + 0.5)}$] and percentage data (fertility) was transformed to arcsine square root prior to analyses (Zar, 1999). The transformed data were analysed using Student's *t*-test to detect differences between both species. Nevertheless, untransformed means (\pm SE) are shown in figures to ease interpretation. Statistical analyses were performed using Infostat version 2015p (Di Rienzo *et al.*, 2008).

Results

Biological and reproductive parameters

In total, 37 and 20 parental crosses were used to determine reproductive parameters of *H. armigera* and *H. zea*, respectively. The duration of each life stage and reproductive parameters are presented in table 1.

Significant differences were found in most of biological and reproductive parameters between *H. armigera* and *H. zea*. Egg, larval and postoviposition duration was longer in *H. zea* than *H. armigera* [egg (t-test, $t = -32.6$; $df = 149$; $P < 0.0001$), larva (t-test, $t = -45.5$; $df = 139$; $P < 0.0001$), postoviposition period (t-test, $t = -7.6$; $df = 55$; $P < 0.0001$)]. Preoviposition and oviposition duration was longer in *H. armigera* than *H. zea* [preoviposition period (t-test, $t = 11.8$ $df = 55$; $P < 0.0001$), oviposition period (t-test, $t = 5.41$ $df = 54$; $P < 0.0001$)]. *H. armigera* had a higher fertility (t-test, $t = 2.6$; $df = 28$; $P = 0.015$) (table 1).

Life tables and population parameters

Population parameters of both species are shown in table 2. The only parameter that did not differ between *H. armigera* and *H. zea* was the net reproductive rate (R_0) (t-test, $t = -1.35$; $df = 55$; $P = 0.18$). The R_0 for *H. armigera* and *H. zea* was 96.95 and 104.78 which indicates that one female could produce, on average, other 96.95 ± 7.62 and 104.78 ± 4.86 new females during their lifetime respectively. Because “ R_0 ” values were greater than 1.0 for both species, the two populations under controlled environmental conditions increased in size (table 2).

The relation between age-specific fertility (m_x) and age-specific survival (l_x) is illustrated in figure 1 and 2 for both species. The maximum rate of population growth occurred in the day 34 and in the day 46 for *H. armigera* (figure 1) and *H. zea* (figure 2) respectively. Fertility was higher for *H. zea* than *H. armigera*.

Fecundity had four peaks at days 34, 36, 38 and 42 of *H. armigera*'s life cycle. In the case of *H. zea*, fecundity had two peaks: one at day 42 and the other at day 45 of its life cycle.

Table 1. Biological and reproductive parameters of *H. armigera* and *H. zea* populations collected in Argentina and reared with artificial diet at 27 ± 2 °C, 70-75% RH and 14L:10D.

	<i>Helicoverpa armigera</i>				<i>Helicoverpa zea</i>			
	Duration	Range	Survivorship (%)	N	Duration	Range	Survivorship (%)	N
Egg	3.53 ± 0.03a	3-4	100	218	6.46 ± 0.09b	4-7	100	110
L1	2.56 ± 0.05a	2-6	73.85	161	4.13 ± 0.05b	4-5	47.27	52
L2	3.42 ± 0.08a	2-7	72.93	159	3.69 ± 0.11b	3-5	38.18	42
L3	3.4 ± 0.1a	2-8	70.64	154	4.43 ± 0.16b	2-6	38.18	42
L4	4.13 ± 0.14a	2-8	49.54	108	5.31 ± 0.08b	4-6	38.18	42
L5	3.37 ± 0.29 ⁽¹⁾	1-6	8.71	19	2.66 ± 0.1	2-4	38.18	42
L6	5.67 ± 2.19 ⁽¹⁾	3-10	1.37	3	4.22 ± 0.09	2-5	37.27	41
Overall larval stage	12.56 ± 0.2a	9-20	53.67	108	24.51 ± 0.11b	23-26	37.27	41
Pupa	11.98 ± 0.13a	9-14	36.69	80	12.37 ± 0.21a	10-15	37.27	41
Female longevity	13.63 ± 0.59a	6-20	19.26	42	12.75 ± 0.95a	7-18	19.09	21
Male longevity	12.83 ± 0.62a	6-20	17.43	38	12.65 ± 0.89a	7-18	18.18	20
Sex ratio ♀:♂	1:0.9	-	-	-	1:0.8	-	-	-
Pre-oviposition period	4.86 ± 0.23a	3-8	-	37	1.45 ± 0.15b	1-3	-	20
Oviposition period	7.14 ± 0.67a	1-14	-	37	3.1 ± 0.29b	2-6	-	20
Post-oviposition period	1.95 ± 0.35a	0-9	-	37	8.2 ± 0.93b	2-14	-	20
Total fecundity	328.84 ± 22.99a	85-669	-	37	349.2 ± 16.44a	255-482	-	20
Total fertility	96.46 ± 0.64a	76.47-100	-	37	92.16 ± 1.98b	68.7-99.1	-	20

Values followed by same letters within a row are not significantly different according to Student's t-test ($P > 0.05$).

⁽¹⁾The duration of L5 and L6 of *H. armigera* were not consider in the overall larval stage.

Table 2. Population parameters of *H. armigera* and *H. zea* reared with artificial diet at 27 ± 2 °C, 70-75% RH and 14L:10D.

	R_0	T	r	DT	λ
<i>Helicoverpa armigera</i>	96.95 ± 7.62 a	37.59 ± 0.35a	0.12 ± 0.0019a	5.9 ± 0.1a	1.13 ± 0.0021a
<i>Helicoverpa zea</i>	104.78 ± 4.86a	46.86 ± 0.21b	0.1 ± 0.0011b	7.03 ± 0.07b	1.1 ± 0.0012b

Values followed by same letters within a column are not significantly different according to Student's t-test ($P > 0.05$).

R_0 : net reproductive rate, T: time interval between generations (days), r: intrinsic rate of increase (females/female/day), DT: population doubling time (days), λ : finite rate of increase (days).

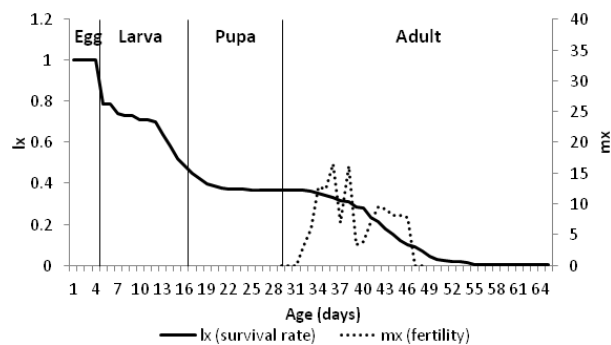


Figure 1. Relationship between fertility (mx) and survival rate (lx) of *H. armigera* reared with artificial diet at 27 ± 2 °C, 70-75% RH and 14L:10D.

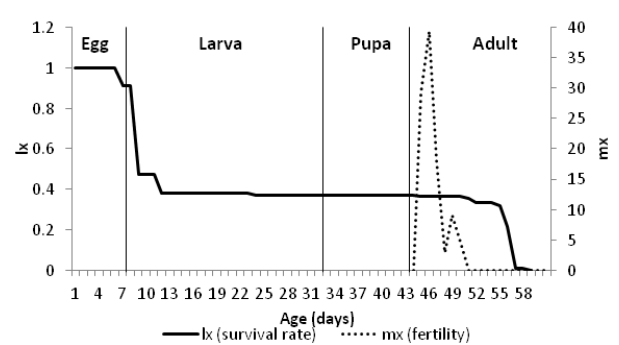


Figure 2. Relationship between fertility (mx) and survival rate (lx) of *H. zea* reared with artificial diet at 27 ± 2 °C, 70-75% RH and 14L:10D.

Gross fecundity rate was 328.84 ± 22.99 and 349.2 ± 16.44 of *H. armigera* and *H. zea* respectively and net fecundity rate was 319.27 ± 23.8 and 322.55 ± 17.3 of *H. armigera* and *H. zea* respectively. The differences between gross and net fecundity rates were not significant for both species (figure 3 and 4). The average number of eggs laid per day was 22.4 ± 4.02 and 19.4 ± 9.16 for *H. armigera* and *H. zea* respectively and the differences

were not significant. Daily gross and net fecundity curves are shown in figure 3 and 4.

Considering the survival analysis (figure 1 and 2), out of the 218 eggs reared on artificial diet, only 80 individuals (36.69%) of the *H. armigera* reached the adult stage (table 1). Females and males had similar survival; out of the total of individuals that reached the adult stage, 19.26% were females and 17.43% were males.

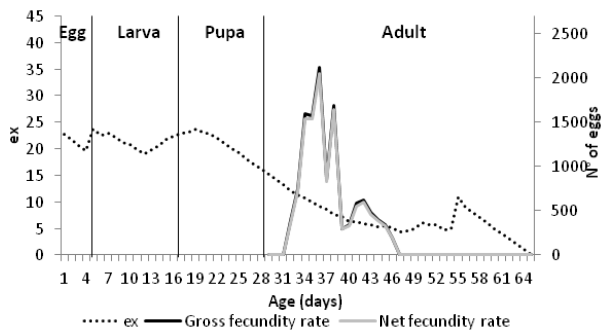


Figure 3. Life expectancy (*ex*), daily gross and net fecundity of individuals of *H. armigera* reared with artificial diet at 27 ± 2 °C, 70-75% RH and 14L:10D.

The life expectancy (*ex*) curve showed three periods of mortality (figure 3 and 4). The highest one occurred from egg stage to first larval instar; the second period occurred from third to fourth instar, and the third one occurred from larval to pupa stage.

Similar to *H. armigera*, out of the 110 eggs only 41 individuals (37.27%) of *H. zea* reached the adult stage (table 1, figure 3 and 4) and 19.09 and 18.18% were female and male respectively.

The life expectancy curve showed two periods of high mortality for this species (figure 3 and 4). The first period was from egg stage to first larval instar and the second period occurred from the first to second instar.

Biotic potential

The BP of *H. armigera* was higher than that of *H. zea*. Considering a 0.53 and 0.55 sex ratio, no environmental resistance, and the following values for the components of the BP equation, $d = 319.3$ and 322.5 ; and $n = 8.7$ and 6.51 , BP of *H. armigera* and *H. zea* was 3.67×10^{19} and 4.54×10^{14} individuals/female/year respectively.

Discussion

This study provides for first time a comparative study about biological, reproductive and population parameters between *H. armigera* and *H. zea* populations from Argentina reared on artificial diet.

Most of biological, reproductive and population parameters of both species varied significantly. However pupa duration, female and male longevity, total fecundity, and Ro were similar for both species.

Results of our study show that *H. armigera* and *H. zea* takes 41.86 ± 0.56 and 56 ± 0.95 days, respectively to complete a single generation (from egg to adult) under controlled environmental conditions.

Larval developmental can vary widely depending on rearing conditions (temperature, humidity, etc.), host diet, or host phenology. Temperature and humidity have been recognized as important factors affecting life history of lepidopterans (Boldt *et al.*, 1975; Sandhu *et al.*, 2010; Tamiru *et al.*, 2012). Studies of these species discussed here were performed under similar environmental conditions (temperatures 25-26 °C and humidity ranged

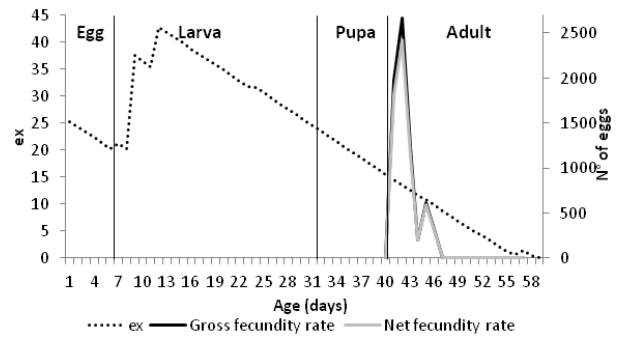


Figure 4. Life expectancy (*ex*), daily gross and net fecundity of individuals of *H. zea* reared with artificial diet at 27 ± 2 °C, 70-75% RH and 14L:10D.

from 50 to 80%) to those used in our study. However, host-plant nutritional value has also been proposed among other factors affecting survivorship of development stages (Pereyra and Sanchez, 2006). In this case, all studies considered here used different host diets (artificial diet and/or host plants). Studies that used artificial diets included chickpea or common bean flour as principal component (Giolo *et al.*, 2006; Silveira Garcia *et al.*, 2006; Amer and El-Sayed, 2014; Barbosa *et al.*, 2016; Nunes *et al.*, 2017; Gomes *et al.*, 2017). In general, the ingredients of these diets were similar to that used in our study. The other studies used different species of host plants to evaluate their effect on development of *H. armigera* and *H. zea*. The hosts plant used were cotton, okra fruit (*Hibiscus esculentus*), maize, castor bean (*Ricinus communis*), pea (*Pisum sativum*), bean (*Phaseolus vulgaris*), soybean, rattlepods (*Crotalaria spectabilis*), millet (*Pennisetum glaucum*), sorghum (*Sorghum bicolor*), cowpea (*Vigna unguiculata*), wheat, tomato, hot pepper (*Capsicum frutescens*), tobacco, chickpea, and asparagus (*Asparagus officinalis*) (Liu *et al.*, 2004; Singh and Yadav, 2009; Jha *et al.*, 2012; 2014; Amer and El-Sayed, 2014; Reigada *et al.*, 2016; Deb and Bharpoda, 2016; Gomes *et al.*, 2017).

Eggs duration was 3.53 ± 0.03 and 6.46 ± 0.09 days for *H. armigera* and *H. zea* respectively. Regardless of the diets used, egg duration of *H. armigera*, was similar to those reported by Liu *et al.* (2004), Jha *et al.* (2012), Nunes *et al.* (2017), Gomes *et al.* (2017). For *H. zea*, the duration of egg was longer than reported by others (Capinera, 2000; Navarro *et al.*, 2009; Tulli *et al.*, 2016). It is important to mention that last authors did not specify the diet used and the study of Tulli *et al.* (2016) was performed under natural environmental conditions.

Four and six larval instars of *H. armigera* and *H. zea* were found and these results were similar to that reported by Butler (1976), Capinera (2000), Jha *et al.* (2012), Liu *et al.* (2004), Barbosa *et al.* (2016), Reigada *et al.* (2016) and Tulli *et al.* (2016). Larval developmental time was 12 and 24 days for *H. armigera* and *H. zea* respectively. These values are within the range of values reported by other authors for both species according the diet or temperature conditions used (Butler, 1976; Capinera, 2000; Giolo *et al.*, 2006; Navarro *et al.*, 2009; Jha *et al.*, 2012; Amer and El-Sayed, 2014; Barbosa *et al.*, 2016; Deb and

Bharpoda, 2016; Reigada *et al.*, 2016; Tulli *et al.*, 2016; Gomes *et al.*, 2017; Nunes *et al.*, 2017). In general, the use of artificial diets rather than different host plants as natural diets as those mentioned in this study appears to shorten the larval and pupal periods for both species. Considering the natural diets for *H. armigera*, some studies reported here revealed that cotton and soybean can be the most appropriate for rearing this species according to the viability at the stages of growth (Liu *et al.* 2004; Amer and El-Sayed, 2014; Reigada *et al.*, 2016; Gomes *et al.*, 2017).

Pupal stage duration for both species was similar to those reported by other studies (Butler, 1976; Capinera, 2000; Liu *et al.*, 2004; Giolo *et al.*, 2006; Navarro *et al.*, 2009; Jha *et al.*, 2012; 2014; Amer and El-Sayed, 2014; Reigada *et al.*, 2016; Nunes *et al.*, 2017; Gomes *et al.*, 2017).

Adult longevity and resulting reproductive qualities may vary according to the nutritional quality of the larval diet and the adult food. Varying the sugar concentration in the adult diet may affect one species of Lepidoptera but not another (Sharma and Chaudhary, 1985). Among numerous nutrients (notably, proteins, carbohydrates, lipids, vitamins, and mineral elements), it seems that carbohydrate is the most important ingredient in the adult diet affecting egg production and survival of many adult Lepidoptera. Apparently, much of the moths' dietary requirement is obtained during the larval stage (Simmons and Lynch, 1990). All studies considered here used a solution of water and honey at 10 or 30% for feeding the adults. Therefore, the differences found in longevity and oviposition for *H. armigera* and *H. zea* may be due to the larva diet used.

Adults from *H. armigera* and *H. zea* had a similar longevity as those reported by Simmons and Lynch (1990), Liu *et al.* (2004), Giolo *et al.* (2006), Silva *et al.* (2017) and Capinera (2000). Other authors reported higher values (Jha *et al.*, 2012; 2014; Reigada *et al.*, 2016; Gomes *et al.*, 2017; Nunes *et al.*, 2017). The sex ratio found for *H. armigera* (1 female: 0.9 male) and *H. zea* (1 female: 0.8 male) was similar to those reported by Giolo *et al.* (2006), Jha *et al.* (2012; 2014), Reigada *et al.* (2016), Gomes *et al.* (2017), Nunes *et al.* (2017).

The duration of pre-oviposition period of *H. armigera* was similar to that reported by Gomes *et al.* (2017) and Silva *et al.* (2017) but differed with the values found by other authors (Jha *et al.*, 2012; 2014; Amer and El-Sayed, 2014; Nunes *et al.*, 2017). Our values of oviposition and postoviposition of *H. armigera* were similar to those reported by Amer and El-Sayed (2014), and Silva *et al.* (2017), but were higher than those reported by Jha *et al.* (2014), Gomes *et al.* (2017) and Nunes *et al.* (2017). In the case of *H. zea*, showed a pre-oviposition and oviposition periods shorter than found by Simmons and Lynch (1990) and Giolo *et al.* (2006) and the postoviposition periods was longer than that reported by the last authors.

Several authors reported higher fecundity of *H. armigera* and *H. zea* than those recorded in our study (Simmons and Lynch, 1990; Capinera, 2000; Liu *et al.*, 2004; Gomes *et al.*, 2017; Nunes *et al.*, 2017; Silva *et al.*, 2017). However, our fecundity results for both species were similar to those found by Jha *et al.* (2012), Giolo *et al.*

(2006), Navarro *et al.* (2009), Amer and El-Sayed (2014) and Reigada *et al.* (2016).

Our fertility results of *H. armigera* showed values higher than those reported by Amer and El-Sayed (2014), Reigada *et al.* (2016) and Silva *et al.* (2017). The value of *H. zea* fertility found in this study was similar to that reported by Navarro (1987) and lower than those reported by Simmons and Lynch (1990).

The net reproductive rate (R_0) of females of *H. armigera* was lower than those reported by Silveira Garcia *et al.* (2006), Naseri *et al.* (2009), Singh and Yadav (2009), Deb and Bharpoda (2016), Silva *et al.* (2017), Nunes *et al.* (2017), Gomes *et al.* (2017) but it was similar to those reported by Liu *et al.* (2004) and Jha *et al.* (2012). *H. zea* R_0 obtained in our study was different to that reported by Silveira Garcia *et al.* (2006). These authors found that one female produced 41.9 and 224 new females during their lifetime using two artificial diets. The intrinsic rate of increase (r) and the finite rate of population increase (λ) of *H. armigera* and *H. zea*, showed similar values to those reported by other authors (Silveira Garcia *et al.*, 2006; Singh and Yadav 2009; Naseri *et al.*, 2009; Jha *et al.*, 2012; 2014; Choudhury *et al.*, 2012; Razmjou, 2013; Deb and Bharpoda, 2016; Nunes *et al.*, 2017; Silva *et al.*, 2017). Time elapsed between generations (T) of *H. armigera* and *H. zea* was in general similar than those found by others (Silveira Garcia *et al.*, 2006; Singh and Yadav 2009; Naseri *et al.*, 2009; Jha *et al.*, 2012; Deb and Bharpoda, 2016; Nunes *et al.*, 2017; Silva *et al.*, 2017). The time taken for the population of *H. armigera* to double in size (DT) was similar to those reported by Naseri *et al.* (2009), Choudhury *et al.* (2012) and Razmjou *et al.* (2013) but it was higher than that reported by Gomes *et al.* (2017). No previous studies have examined the population doubling time of *H. zea*, but in general it was similar to those observed for *H. armigera*.

The BP of *H. armigera* and *H. zea* indicate that each female can produce more than 36 quintillion and 454 trillion descendants respectively. The BP of *H. armigera* was similar to that obtained by Herrero *et al.* (2018) for *H. gelotopoeon* but it was lower those obtained by Silva *et al.* (2017) for *H. armigera* from three Brazilian regions. This difference could be due to the origin of the populations since the insects were reared on artificial diet and laboratory conditions similar to those used in this study. No previous studies have examined the BP of *H. zea*, but in general it was lower to those observed for *H. armigera* and *H. gelotopoeon*.

The life expectancy curve (ex) indicated the critical ages of mortality. Individuals of *H. armigera* (egg until fourth larval instar) and *H. zea* (egg until second larval instar) reared on artificial diet revealed higher mortality at early stages. These results are consistent with Liu *et al.* (2004) and Herrero *et al.* (2018), who found that larval mortalities of *H. armigera* and *H. gelotopoeon* respectively were higher between 1-3 instars for the host plants or artificial diet tested. Vargas and Nishida (1980) observed the same trend for *H. zea* and Tulli *et al.* (2016) reported that the egg stage of *H. zea* showed the higher mortality percentage in corncoobs in natural conditions.

The survivorship curve (lx) of *H. armigera* and *H. zea* resemble the theoretical type III (showing that there is a

constant fraction of living individuals that die in each life stage) and type IV (showing higher mortality rate during the egg stage and first larval instars, then, it declined slowly until the death of last adult) (Rabinovich, 1978) respectively. For both species, our results are similar to those obtained by Jha *et al.* (2014) for *H. armigera* and Herrero *et al.* (2018) for *H. gelotopoeon* who found that only the half of the individuals of these species completed their larval stage and survived to pupal stage. In the case of *H. zea*, Vargas and Nishida (1980) reported that from 100% of the eggs only 70% of them reached adult stage in controlled environmental conditions.

The maximum mean progenies production (*mx*)/day was 16.46 and 39.34 females/female on the 36th and 46th day of *H. armigera* and *H. zea* life respectively. The value obtained for *H. armigera* was lower than that found by other authors (Naseri *et al.*, 2009; Singh and Yadav, 2009, Deb and Bharpoda, 2016) who found values ranging from 46 to 159 females/female for this species. The *mx*/day of *H. zea* was similar to that reported by Silveira Garcia *et al.* (2006).

The mean fecundity of *H. armigera* and *H. zea* was 319.27 and 322.55 fertile eggs/female respectively, which is lower than that observed for *H. armigera* by Silva *et al.* (2017) and for *H. gelotopoeon* by Herrero *et al.* (2018). The differences between number of eggs laid with respect to the number of eggs hatched were not significant for both species. These values were lower than those reported by Naseri *et al.* (2011) and Hemati *et al.* (2013) for *H. armigera* and by Herrero *et al.* (2018) for *H. gelotopoeon*. No previous studies have examined *H. zea* gross and net fertility but in general they were smaller than those reported by *H. armigera* and *H. gelotopoeon* (Naseri *et al.*, 2011; Hemati *et al.*, 2013; Herrero *et al.*, 2018).

Similar to Barbosa *et al.* (2016), the present study showed that *H. armigera* has a shorter life cycle than *H. zea*, which suggests a greater number of generations per year and faster population growth. On the other hand, the BP obtained for each species indicated the potential economic losses that these species could cause to a wide variety of crops species. In the case of highly polyphagous species such as *H. armigera*, the knowledge of BP is additionally important to predict the differences in its development according to the plant species it feed. Studies made by Murúa *et al.* (2016) showed that *H. armigera* had a seasonal distribution in chickpea and soybean crops in Tucumán province (Argentina), being more prevalent in September and October on chickpea and during February and March on soybean. This information would indicate that first infestations in soybean crops are produced by adults emerged from chickpea crops. Thus, more studies are necessary to know the performance and BP of *H. armigera* feeding on soybean and chickpea to generate information for management of this species in agricultural ecosystems.

Considering the results obtained in this study, they may provide additional information that can be used to plan and implement strategies for the integrated management of these species with emphasis in *H. armigera* in Argentina.

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