



Biology, Ecology and Diversity

The population dynamics of three polyphagous owlet moths (Lepidoptera: Noctuidae) and the influence of meteorological factors and ENSO on them


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ABSTRACT

The owlet moths (Lepidoptera: Noctuidae) *Anicla infecta* (Ochsenheimer 1816), *Elaphria agrotina* (Guenée 1852) and *Spodoptera frugiperda* (J.E. Smith 1797) occur in the entire American continent. These polyphagous moths have a preference for grasses, and have different biological habits. In this study, the populations of these three species were evaluated monthly with light traps in the Brazilian Savannah, ranging a span of four crop seasons (from July, 2013 to June, 2017). The population data were analyzed and correlated with the meteorological variables: maximum temperature, minimum temperature, relative humidity and precipitation. A total of 4719 individuals were collected in the following percentages: *A. infecta* (n = 459; 9.73%), *E. agrotina* (n = 1809; 38.33%) and *S. frugiperda* (n = 2451; 51.94%). The abundance of all species went down from the first crop season (2013/2014) to the third (2015/2016). In the fourth crop season (2016/2017), the populations of *A. infecta* and *E. agrotina* stabilized, but the abundance of *S. frugiperda* experienced further decrease. The numbers of individuals of three species declined when precipitation was much above (crop season 2014/2015) and below (crop season 2015/2016) than expected by the climatological normal. There were significant, but different degrees of correlation, between the meteorological factors and the ONI index (Oceanic Niño Index - indicator for monitoring El Niño-Southern Oscillation or “ENSO”) with respect to monthly population variations. The results are discussed in accordance with principles of the Integrated Pest Management (IPM) in mind, given the continental distribution and agricultural importance of the three owlet moth species studied.

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Introduction

Insects are very diverse and play fundamental roles in ecosystems. Adult lepidopterans (butterflies and moths) are important pollinators of wild plants and also many food crops (Kondo, 2012). Their larvae, in contrast, have a great negative impact on plants, eating their leaves, flowers, fruits, seeds, branches and even roots (Weisse and Siemann, 2008). Out of their natural habitat lepidopterans can become important pests. The owlet moths, *Anicla infecta* (Ochsenheimer, 1816), *Elaphria agrotina* (Guenée, 1852) and *Spodoptera frugiperda* (J.E. Smith, 1797) are good examples of this. They occur throughout the American continent and recently, *S. frugiperda* has also been detected in the African continent (Goergen

et al., 2016), Europe (CABI, 2017) and India (Shylesha et al., 2018). Their caterpillars are polyphagous, with a strong preference for grasses (Teston et al., 2001; Lafontaine, 2004; Casmuz et al., 2010; Specht et al., 2014; Montezano et al., 2018). The caterpillar of *A. infecta* feeds preferentially on the foliar limb of native and cultivated grasses such as oats, ryegrass, grasses, millet and corn (Teston et al., 2001). *Elaphria agrotina* stays in the soil and eats debris/tillage or dead plant structures of crops such as maize, including leaves, cobs, stigmas and dried seeds (Specht et al., 2014). *Spodoptera frugiperda* has a polyphagous caterpillar which can be a pest of many crops, including monocotyledonous and dicotyledonous plants. In cultivated Poaceae, it prefers young leaflets (attacking the maize, millet and sorghum husk), but also attacks reproductive tissues (such as corn ear or panicle of millet and sorghum) (Montezano et al., 2018). When their population numbers are high, they are considered pests due to their negative impact on the production of some crops (Capinera, 2008).

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Lepidopteran pests cause losses not only by impairing plant production, but also by requiring expensive management (Paula-Moraes et al., 2017). The knowledge of the relationships between the population fluctuations of each species with the meteorological variations can contribute with data for the development of forecasting systems, promoting the rationalization of their management (Zalucki and Furlong, 2005). In this way, this work presents and compares the population dynamics of *A. infecta*, *E. agrotina* and *S. frugiperda* in four crop seasons in Central Brazil, considering the Oceanic Niño Index (ONI) climatic pattern as a possible influence on it.

Materials and methods

Study area

This study was carried out in the area of 'Estação Experimental da Embrapa Cerrados', located in the city of Planaltina, Distrito Federal, Brazil, which is predominantly an agricultural area. It is located in the 'Cerrado' biome (Ab'Saber, 2003), also known as the Brazilian Savannah. According to the climate classification of Köppen, it has a Tropical Wet-Dry Climate (Aw), with average temperatures around 17 °C in the coldest and 22 °C in the hottest months. The region is marked by two seasons, defined by the differences in rainfall accumulation. The rainy period starts in September and extends until April. The wettest months are November, December and January. The dry period starts in May and ends in September, resulting in a hot and rainy summer and mild and dry winter (Silva et al., 2017).

The sampled landscape is totally surrounded by native vegetation of Brazilian Savannah, but in the collecting point there are several agriculturally important crops, especially soybean, corn and wheat, which occupy about 25, 15 and 10% of the 400-meter radius from the collecting site. Part of the area is occupied with agricultural buildings (barns and greenhouses) and, to a lesser extent, crops of other species such as bluestem, coffee, cassava, rattleweed, gum, oil palm, panicgrass, passion fruit and sugar cane. Wheat, soybean and corn stand out because the former is restricted to the dry period, while the other two are restricted to the rainy season. It is assumed that other crops do not affect the phenology of *A. infecta*, *E. agrotina* and *S. frugiperda* because they are perennial plants which are not preferential hosts for these species, and/or are cultivated in small areas. During four crop seasons the crops were repeated to avoid changing the availability of food for the owlet caterpillars.

Meteorological data and Oceanic Niño Index (ONI)

The meteorological data was obtained from the Estação Climatológica Principal da Embrapa Cerrados with meteorological sensors at a distance of 20 m from the light trap. The variables analyzed were maximum (Tmax) and minimum (Tmin) temperature, relative humidity (RH) and precipitation (Precip). The Oceanic Niño Index (ONI) values were obtained in NOAA (2018). The Oceanic Niño Index (ONI) is NOAA's primary indicator for monitoring El Niño and La Niña, which are opposite phases of the climate pattern called the El Niño-Southern Oscillation or "ENSO" for short. NOAA considers El Niño conditions to be present when the ONI is +0.5 or higher, indicating the East-Central Tropical Pacific is significantly warmer than usual. On the other hand, La Niña conditions exist when the ONI is -0.5 or lower, indicating that the region is cooler than usual. Values over 0.5 correspond to El Niño and under -0.5 correspond to La Niña.

Insect collecting

The moths were collected with a Pennsylvania light trap (Frost, 1957) at the following coordinates 15°35'30" S and 47°42'30" W,

altitude: 1007 m a.s.l. This trap was equipped with a black fluorescent light model BL T8 15 W (Tovalight) and was lit during five nights at each *novilunium*, to minimize the moonlight effects on trap efficiency. Each night is considered a repetition in the analysis, and the insects collected each night per *novilunium*/month were individualized to calculate the means. This trap was placed three meters from the ground, inside the crop area.

In total, the trap was lit 50 times over a period of four years in *novilunium* to represent all months during that period. The collecting activities started in July when the harvest period starts and ended in June of the following year. Therefore, in the present study we considered four crop seasons, from June of 2013 to July of 2017. Crop season 1 (CS1) – July of 2013 to June of 2014; crop season 2 (CS2) – July of 2014 to June of 2015; crop season 3 (CS3) – July of 2015 to June of 2016 and crop season 4 (CS4) – July of 2016 to June of 2017.

Due to an excess of rainfall and a large number of Coleoptera, Hymenoptera and Isoptera attracted to the trap in November, 2013, the owlet moths were damaged to the point that their identification was not possible. For this reason, the samples collected on that month were not considered. In the months when there were two new moons, July 2015 and September 2016, the collecting process was considered a repetition. Therefore, instead of considering the usual five collections, we considered ten for the same month. The identification of insects during the sorting process was based on the literature (Angulo and Olivares, 1997; Pogue, 2002; Specht et al., 2014). The specimens were preserved in ethanol (96%), and representative vouchers were pinned and deposited in the Entomological Collection of Embrapa Cerrados.

Statistical analysis

Three separate analyses were conducted, one for each species: *A. infecta*, *E. agrotina* and *S. frugiperda*, for four years with entirely randomized design and five temporal repetitions. The analysis has two qualitative factors: crop season (four crop seasons) and months (twelve).

Normality of variances was tested annually using the Shapiro-Wilk. T-test was used to compare differences in the average abundance among the crop seasons. A Generalized Linear Model (GLM) Poisson Regression was used to determine how the mean expected value of a continuous response variable (abundance) depends on a set of explanatory variables (daily meteorological factors). To complement this, another similar analysis was conducted, comparing the monthly means of the populations of each species with ONI data (Oceanic Niño Index). The Poisson regression model takes into account discrete variables. The analysis using this regression model involved the total number of individuals of *A. infecta*, *E. agrotina* and *S. frugiperda* collected in each sample (McCullagh and Nelder, 1989). It works with non-normality distributions by modeling the data and identifying problems with discreteness in the outcomes (e.g. the "lump" of zeros) (Vittinhoff et al., 2004).

Data were analyzed and graphed using the R Software ver. 3.3.1, Action Stat Module.

Results

Abundance of species according crop seasons

In general, the results indicate that all populations of the three species decreased in numbers from CS1 to CS4 (Table 1, Fig. 1) with significant differences between CSs ($p < 0.05$). There were two exceptions: non-significant variations in the number of individuals were observed for *A. infecta* between CS3 and CS4 ($p = 0.77$) and for *E. agrotina* between CS2 and CS4 ($p = 0.20$) and CS3 and CS4 ($p = 0.91$).

Table 1
Specific abundance of three owl moth species in four crop seasons: July of 2013 to June of 2017 (CS1 - 2013/2014, CS2 - 2014/2015, CS3 - 2015/2016, CS4 - 2016/2017). T-test comparisons performed using mean number (five nights) of moths captured with light traps in each crop season (60 nights) at Embrapa Cerrados, Federal District, Brazil.

Species	Specific abundance					P value					
	CS1	CS2	CS3	CS4	Total	CS1 × CS2	CS1 × CS3	CS1 × CS4	CS2 × CS3	CS2 × CS4	CS3 × CS4
<i>Anicla infecta</i>	296	102	30	31	459	0.00	0.00	0.00	0.02	0.04	0.77
<i>Elaphria agrotina</i>	1516	183	55	55	1809	0.00	0.00	0.00	0.02	0.20	0.91
<i>Spodoptera frugiperda</i>	1337	786	221	107	2451	0.00	0.00	0.00	0.04	0.00	0.02
Total	3149	1071	306	193	4719	-	-	-	-	-	-

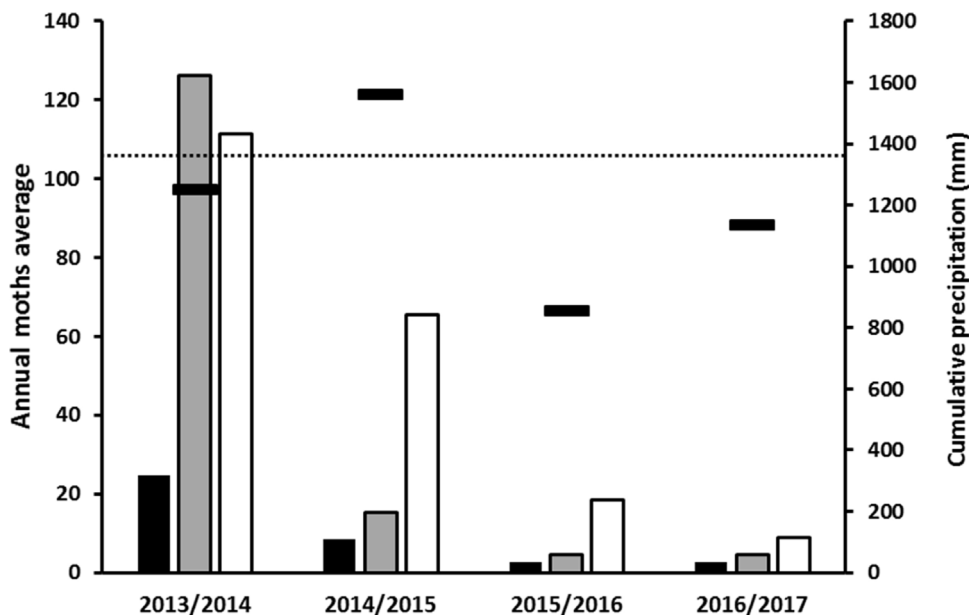


Fig. 1. Annual average abundance of *Anicla infecta* (black columns), *Elaphria agrotina* (grey columns) and *Spodoptera frugiperda* (white columns); cumulative precipitation in cubic millimeters per quadratic meter (black bars) in four Crop Seasons and expected precipitation according to Climatological Normal 1974–2004 (Silva et al., 2014). Moths captured with light traps at Estação Experimental da Embrapa Cerrados, Federal District, Brazil.

Regarding to the variations in populations per species during and among the crop seasons, the following results are notable:

The average number of individuals of *A. infecta* decreased from 24.7 (CS1) to 8.5 in CS2 and to 2.5 in CS3 (Fig. 1). Similarly, and despite the fact that comparisons involving November's CS1 were not possible, significant monthly decreases in numbers of individuals were observed, particularly between CS1 and CS2, CS3 and CS4 (Table 2, Fig. 2a).

The average number of *E. agrotina* individuals decreased from CS1 (126.3), to CS2 (12.3), to CS3 (4.6) and remained stable in CS4 (4.6) (Fig. 1). With respect to the monthly fluctuations between crop seasons showed that July of 2013 (CS1) was the month when there were more individuals collected, with an average total of 106.3 moths per night (Table 2). In most cases, there was a decrease in abundance from one crop season to another, such as in July 2013, when there was a decrease of 96.05% in the average number of individuals (102.1) compared to CS2 and 99.81% (106.1) compared to CS3 and CS4 (Table 2). Significant decreases were also observed in at least half of the months, particularly in the comparisons between CS1 and the other crop seasons (Table 2).

Similarly, for four crop seasons, the total average of individuals of *S. frugiperda* progressively decreased from 111.4 in CS1 to 8.9 in CS4 (Fig. 1). This decrease in population numbers was significant between the harvests of most months, including comparisons with the last harvest (Table 2).

Another important aspect is that all species under study were present (were collected) in practically every month during all four crop seasons. However, the specific monthly abundance of each

species, and the peaks in the population of each species, varied among the crop seasons. This is the case of *A. infecta*, which was more abundant in July, August and September of 2013; April, May and June of 2014. In the case of *E. agrotina*, the greatest numbers of individuals were collected only in July of 2013 and finally, for *S. frugiperda*, the population peak was reached in July of 2013, January, April and November of 2014 (Tables 1 and 2; Fig. 2).

Relationship between meteorological factors and ONI on the specific abundances

According to our results, indicated by the Poisson coefficients and respective p-values, the climatological variables, except for the minimum temperature on *E. agrotina* and precipitation on *S. frugiperda*, influenced each one of the species in a significant and differential way (Table 3).

Our results indicate that the meteorological variables are negatively correlated with the population numbers of *A. infecta* and *E. agrotina*, meaning that lower population numbers were observed when precipitation, temperature and humidity were at their highest (Table 3).

To *S. frugiperda*, precipitation did not affect the populations in a significant way (Table 3). However, higher maximum temperatures, as observed for *A. infecta* and *E. agrotina*, contributed significantly to a decrease in the numbers of individuals of this species in our samples. The minimum temperature and relative humidity, in contrast, were positively associated with estimated values of abundance, meaning that, an increase in the values of

Table 2

Monthly average abundance of *Anicla infecta*, *Elaphria agrotina* and *Spodoptera frugiperda* in four crop seasons (CS1 - 2013/2014, CS2 - 2014/2015, CS3 - 2015/2016, CS4 - 2016/2017). T-Test comparisons performed with mean number (five nights) of moths captured in light traps by month (five repetitions) at "Estação experimental da Embrapa Cerrados", Federal District, Brazil.

Month	Average abundance					Comparisons between crop seasons											
	CS1	CS2	CS3	CS4	Total	CS1 × CS2	P-val	CS1 × CS3	P-val	CS1 × CS4	P-val	CS2 × CS3	P-val	CS2 × CS4	P-val	C3 × C4	P-val
<i>Anicla infecta</i>																	
J	4.5	2.0	1.0	0	7.5	-2.5	0.00	-3.5	0.00	-4.5	0.00	-1.0	0.11	-2.0	0.00	-1.0	0.03
A	3.4	1.8	0.2	0.2	5.6	-1.6	0.06	-3.2	0.00	-3.2	0.00	-1.6	0.01	-1.6	0.01	0.0	1.00
S	3.8	1.5	0.6	0.5	6.4	-2.3	0.08	-3.2	0.01	-3.3	0.01	-0.9	0.11	-1.0	0.09	-0.1	0.80
O	1.7	0.8	0.6	0.8	3.9	-0.9	0.17	-1.1	0.10	-0.9	0.26	-0.2	0.74	0.0	1.00	0.2	0.79
N	-	0.3	0.0	0.2	0.5	-	-	-	-	-	-	-0.3	0.19	-0.1	0.86	0.2	0.37
D	1.4	0.2	0.4	0.6	2.6	-1.2	0.11	-1.0	0.23	-0.8	0.33	0.2	0.63	0.4	0.37	0.2	0.73
J	1.0	0.1	0.8	0.8	2.7	-0.9	0.03	-0.2	0.70	-0.2	0.74	0.7	0.14	0.7	0.23	0.0	1.00
F	0.8	0.3	0.0	0.2	1.3	-0.5	0.11	-0.8	0.01	-0.6	0.08	-0.3	0.08	-0.1	0.70	0.2	0.37
M	0.8	0.3	0.2	0.6	1.9	-0.5	0.19	-0.6	0.11	-0.2	0.70	-0.1	0.62	0.3	0.56	0.4	0.41
A	4.4	0.7	1.8	0.6	7.5	-3.7	0.00	-2.6	0.02	-3.8	0.00	1.1	0.19	-0.1	0.73	-1.2	0.15
M	2.9	0.4	0.2	0.6	4.1	-2.5	0.00	-2.7	0.00	-2.3	0.00	-0.2	0.67	0.2	0.56	0.4	0.35
J	4.9	1.6	0.1	1.2	7.8	-3.3	0.00	-4.8	0.00	-3.7	0.00	-1.5	0.00	-0.4	0.33	1.1	0.00
<i>Elaphria agrotina</i>																	
J	106.3	4.2	0.2	0.2	110.9	-102.10	0.00	-106.1	0.00	-106.1	0.00	-4.0	0.00	-4.0	0.00	0.0	1.00
A	6.1	2.9	0.0	0.2	9.2	-3.19	0.02	-6.1	0.00	-5.9	0.00	-2.9	0.00	-2.7	0.00	0.2	0.37
S	2.3	1.7	0.0	0.0	4.0	-0.57	0.53	-2.3	0.00	-2.3	0.00	-1.7	0.06	-1.7	0.06	0.0	1.00
O	6.2	1.6	0.4	2.0	10.2	-4.60	0.04	-5.8	0.01	-4.2	0.05	-1.2	0.23	0.4	0.75	1.6	0.13
N	-	1.0	0.6	0.4	2.0	-	-	-	-	-	-	-0.4	0.61	-0.6	0.34	-0.2	0.79
D	1.4	2.5	2.2	0.0	6.1	1.17	0.13	0.8	0.40	-1.4	0.01	-0.3	0.74	-2.5	0.00	-2.2	0.05
J	0.3	0.4	0.8	0.4	1.9	0.07	0.84	0.5	0.60	0.1	0.85	0.4	0.65	0.0	1.00	-0.4	0.65
F	0.5	0.0	1.8	0.2	2.5	-0.45	0.14	1.3	0.08	-0.3	0.47	1.8	0.04	0.2	0.37	-1.6	0.05
M	1.9	0.2	0.8	0.2	3.1	-1.68	0.00	-1.1	0.15	-1.7	0.00	0.6	0.40	0.0	0.94	-0.6	0.38
A	13.7	1.3	1.4	5.6	22.0	-12.43	0.01	-12.3	0.01	-8.1	0.16	0.1	0.86	4.3	0.33	4.2	0.34
M	8.0	0.7	0.6	1.6	10.9	-7.30	0.00	-7.4	0.00	-6.4	0.00	-0.1	0.89	0.9	0.10	1.0	0.12
J	3.9	1.0	1.6	0.2	6.7	-2.90	0.00	-2.3	0.02	-3.7	0.00	0.6	0.33	-0.8	0.08	-1.4	0.02
<i>Spodoptera frugiperda</i>																	
J	21.5	4.8	0.4	0.6	27.3	-16.7	0.00	-21.1	0.00	-20.9	0.00	-4.4	0.00	-4.2	0.00	0.2	0.58
A	7.2	0.0	0.8	1.4	9.4	-7.2	0.00	-6.4	0.00	-5.8	0.00	0.8	0.18	1.4	0.02	0.6	0.37
S	4.2	5.1	0.4	0.25	9.9	0.9	0.54	-3.8	0.00	-4.0	0.00	-4.7	0.00	-4.8	0.00	-0.2	0.68
O	5.8	0.0	0.2	2	8.0	-5.8	0.00	-5.6	0.00	-3.8	0.00	0.2	0.37	2.0	0.02	1.8	0.03
N	-	32.9	1.2	4.4	38.5	-	-	-	-	-	-	-31.7	0.00	-28.5	0.01	3.2	0.11
D	12.4	7.7	14.0	4.2	38.3	-4.6	0.17	1.6	0.74	-8.2	0.03	6.3	0.16	-3.5	0.04	-9.8	0.05
J	22.9	9.7	7.4	1.4	41.4	-13.2	0.03	-15.5	0.02	-21.5	0.00	-2.3	0.47	-8.3	0.00	-6.0	0.10
F	8.1	2.5	3.2	0.8	14.6	-5.6	0.01	-4.9	0.04	-7.3	0.00	0.7	0.62	-1.7	0.02	-2.4	0.13
M	13.3	1.7	10.4	1	26.4	-11.6	0.00	-2.9	0.52	-12.3	0.00	8.7	0.05	-0.7	0.20	-9.4	0.04
A	29.2	3.3	2.2	1.4	36.1	-25.9	0.00	-27.0	0.00	-27.8	0.00	-1.1	0.07	-1.9	0.02	-0.8	0.20
M	0.2	2.0	0.6	3.0	5.8	1.8	0.02	0.4	0.35	2.8	0.19	-1.4	0.14	1.0	0.62	2.4	0.28
J	12.2	0.9	2.4	1	16.5	-11.3	0.00	-9.8	0.01	-11.2	0.00	1.5	0.17	0.1	0.82	-1.4	0.19

Table 3

Coefficients of Poisson Multiple Regression Model calculated for the monthly variations in the mean number of moths collected, considered as predictor variables for climatic factors and ONI (Oceanic Niño Index). Est - Estimate, SE - Standard Error, P - P-value.

Predictor variables	<i>Anicla infecta</i>			<i>Elaphria agrotina</i>			<i>Spodoptera frugiperda</i>		
	Est	SE	P	Est	SE	P	Est	SE	P
Intercept	0.088	0.054	0.107	1.132	0.034	0.000	1.858	0.021	0.000
Maximum temperature	-0.436	0.067	0.000	-1.112	0.035	0.000	-0.238	0.030	0.000
Minimum temperature	-0.119	0.056	0.010	-0.009	0.031	1.000	0.154	0.030	0.000
Relative humidity	-0.423	0.077	0.000	-0.756	0.042	0.000	0.100	0.036	0.001
Precipitation	-0.235	0.103	0.010	-0.271	0.051	0.000	0.024	0.018	1.000
Intercept	0.201	0.143	0.160	1.521	0.073	0.000	1.796	0.065	0.000
ONI	-0.355	0.175	0.042	-1.027	0.129	0.000	-0.141	0.069	0.040

these parameters was significantly associated with increased abundance of *S. frugiperda* in samples (Table 3).

Beyond the meteorological factors, the numbers of individuals of all species were negatively correlated with the ONI values, the primary indicator for monitoring El Niño and La Niña events (Table 3).

Discussion

The consecutive decrease in the abundance of the three owl moth species over the four crop seasons (Table 1; Fig. 1) of this study are consistent with the results obtained for other owl moth species, being *Chrysodeixis includens*, *Spodoptera albula*, *Spodoptera*

cosmioides and *S. frugiperda*, in the same area, in the following crop seasons: 2013/2014, 2014/2015 and 2015/2016 (Piovesan et al., 2017; Santos et al., 2017).

Since this analysis was carried out in a Tropical Savannah (Cerrado) area with two very different seasons (a very long dry season and a very wet season), the temperature (maximum and minimum) fluctuated less than precipitation and relative humidity (Fig. 2). Besides the variations in the observed precipitation values on each crop compared to the expected (Silva et al., 2014), there was a significant drop in precipitation in the fall of 2015/2016, associated with the El Niño. However, in the last crop season (CS4), even without the influence of the El Niño, precipitation and the consequent relative humidity were lower than the annual rainfall

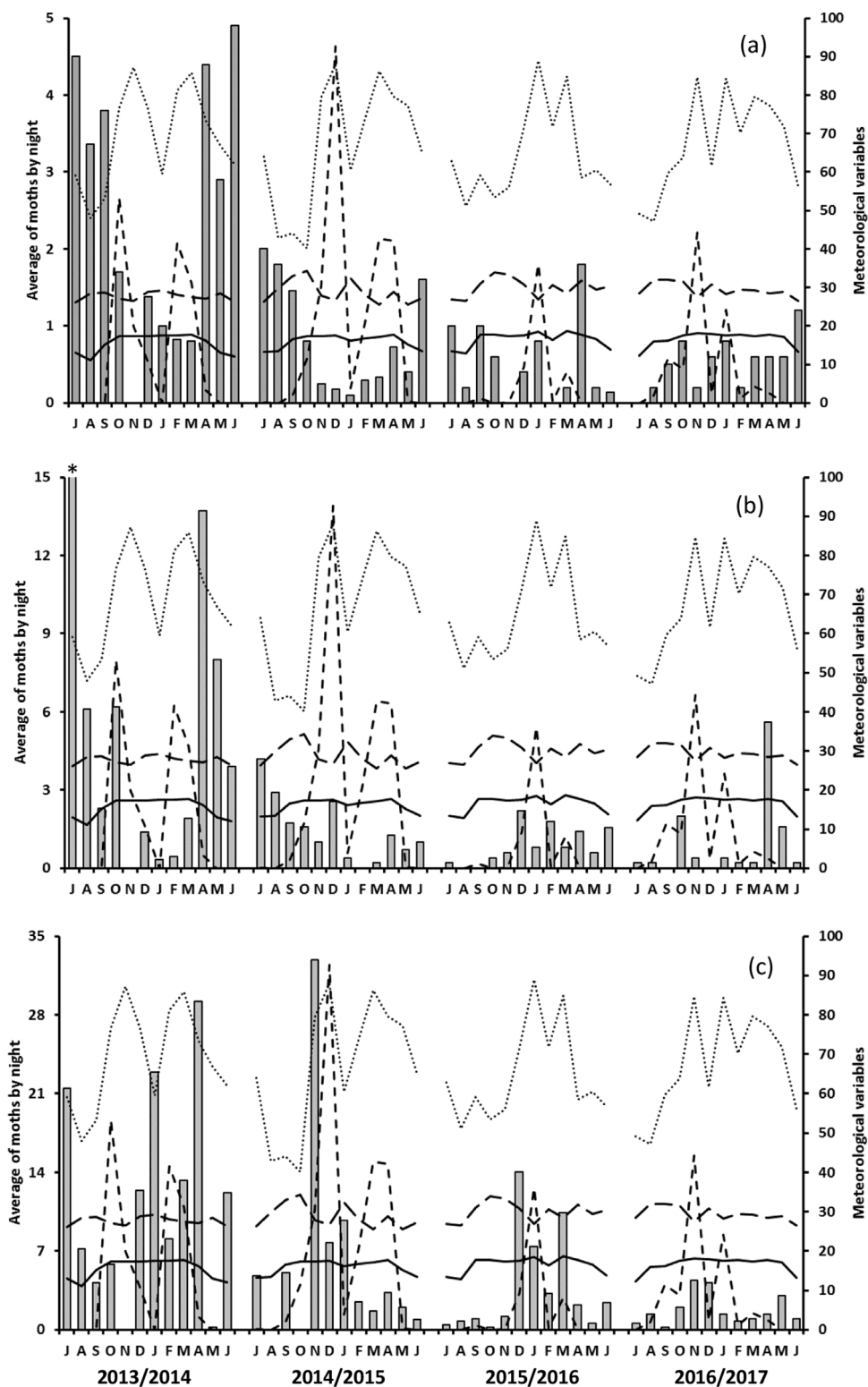


Fig. 2. Average number of moths (a) *Anicla infecta*, (b) *Elaphria agrotina* and (c) *Spodoptera frugiperda* in four crop seasons according to meteorological variables: humidity - dotted line; maximum temperature - long dashed line; minimum temperature - continuous line and precipitation - short dashed line. Left columns have different scales and * [first column of *E. agrotina* (b)] represents 106.3 moths.

volume expected by the climatological normal (Silva et al., 2014, Figs. 1 and 3).

Despite large variations in the volume of precipitation on each crop, according to the Climatological Normal 1974–2004 (Silva et al., 2014), it was not possible to find a connection between the observed decrease in the numbers of individuals of the three species

and volume of precipitation (Table 1, Fig. 1). Species' abundances declined significantly (more than 50%) between the 2013/2014 harvest and the 2014/2015 one, when there was an increase of 19.8% (309.4 mm³) in precipitation. The decrease in the number of individuals, at least in the case of *S. frugiperda*, was as expected, since the caterpillars, especially in the early life stages, tend to drown

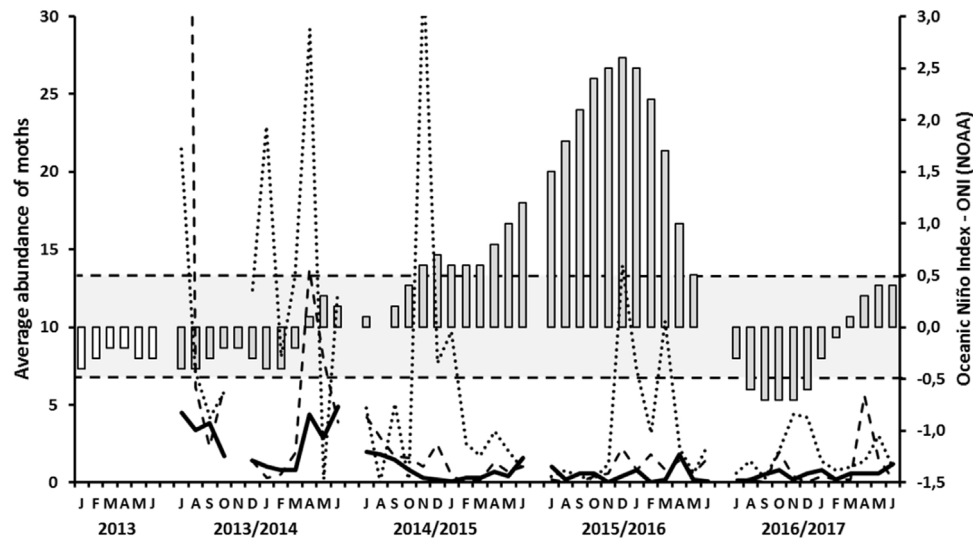


Fig. 3. Average number of *Anicla infecta* (continuous line), *Elaphria agrotina* (dashed line) and *Spodoptera frugiperda* (dotted line) in four crop seasons. Oceanic Niño Index - ONI; the white bars (left) represents six months before the beginning of the collections (gray bars). Values over 0,5 correspond to El Niño and under to -0,5 correspond to La Niña (NOAA, 2018).

inside the corn's cartridge when precipitation is high (its main host plant) (García-Roa et al., 2002). Similarly, the neonate larvae of all the species are, directly or indirectly, highly vulnerable to the impact of raindrops, which can remove them from their host plants (Zalucki et al., 2002). Furthermore, high levels of precipitation, accompanied by high relative humidity, generally induce the occurrence of entomopathogenic epizooties (Ríos-Velasco et al., 2010).

The abundance of the three species continued to drop even more between the 2014/2015 and 2015/2016 crop seasons, when a reduction in precipitation was observed in 54.81% (-705.1 mm³), due to the El Niño phenomenon (Fig. 3). That decrease can be attributed to the extreme water deficit, which among other things, affects the quantity and quality of food available for the insects (Zalucki et al., 2002). Despite this, the abundance decrease in crop season with reduced rainfall differs from the observations reported in the literature where, at least for *S. frugiperda*, the diminution in precipitation would lead to a considerable populational increase, since drier climates favor the larvae of this species (Corte et al., 1985; García-Roa et al., 2002).

In the following crop seasons, between the 2015/2016 and 2016/2017, only the abundance of *S. frugiperda* decreased significantly. It is important to highlight that, although the El Niño event lost its strength, precipitation remained relatively low during the fourth crop season 2016/2017 (1,136.8 mm³) (Figs. 1 and 3). Considering the size of the cultivated area and crop management (same quantity and type of chemical product) over four years and expressive non-intensive agricultural area (3000 ha) around the collecting site, we inferred that the variations in population abundance are linked to other, non-quantifiable elements, such as natural biological control (Pereira et al., 2018).

The fact that the three species were sampled during practically every month of all crop seasons (Table 2, Fig. 2) is conditioned to their multivoltinism, and by the presence, in the study area, of minimal biotic and abiotic conditions for their development and permanence. This also indicates that all species had initial populations (even in the dry season - June to September) that would allow rapid increases in abundance under favorable conditions. However, the monthly abundances of each species within each crop (Table 2, Fig. 2) varied greatly, sometimes with coincident and sometimes antagonistic population peaks, attributed to the behavioral and developmental characteristics of the larvae of each (Kasten et al.,

1978; Teston et al., 2001; Specht et al., 2014). Associated with these variations, the results indicate that the meteorological variables affected the decrease in the numbers of the three species in different ways (Table 3).

The caterpillars of each species have different habits and consume variable food resources (tissues): The caterpillars of *A. infecta* have cryptic coloration (green), rest all day on the leaf limbs and are exposed to daily climatic variations (warmer during the day and cooler at night). Plant tissues commonly consumed (leaves), especially native and cultivated grasses (oats, ryegrass, grasses, millet and corn) tend to be less nutritive (Teston et al., 2001; Lafontaine, 2004). Since they stay close to the leaves, they are relatively more exposed to the attack of natural enemies. *Elaphria agrotina* caterpillars, however, prefer dry plant materials and stay in the soil feeding on debris/tillage or dead plant structures such as maize, including leaves, cobs, stigmas and dried seeds (Specht et al., 2014). Because caterpillars are usually close to the ground, they may or may not feed on nutrient-rich foods (depending on seed availability) and be less exposed to daily variations in temperature and relative humidity and are thus sheltered and protected from natural enemies. At last, *S. frugiperda* caterpillars, although they remain hidden during the day (on the ground or between plant structures), are very mobile from birth and prefer to attack leaves that are starting to develop (attacking the maize, millet and sorghum (Harvey et al., 2008; Casmuz et al., 2010; Favetti et al., 2017). Because they are very mobile, *S. frugiperda* caterpillars are usually sheltered during the day and move out from dusk to early evening to eat, being protected from natural enemies most of the time. This greater mobility still allows their caterpillars (when available) to explore preferred hosts and plant tissues with higher nutritional value, including growing flowers, fruits, seeds or tissues.

Still regarding interspecific variations, the table data shows that the numbers of individuals of *A. infecta* and *E. agrotina* decreased in a similar manner on the three first crops (Table 1) and suffered negative influence of the meteorological parameters that were analyzed (Table 3); but showed differentiated monthly populational variations (Table 2). These divergences between specific monthly abundances were associated with the different degrees of influence of each meteorological parameter (Table 3). We attribute this discrepancy of population variations over time (four crops) and the level of meteorological influence to the different

bioecological aspects of each species (Kasten et al., 1978; Teston et al., 2001; Specht et al., 2014).

It is important to point out in this context is that in the crop season that preceded the first crop of the present study (2012/2013), precipitation was 1229.1 mm³, very similar to the value of crop season 1 (1250.9 mm³), before large precipitation oscillations (Fig. 1) motivated especially by El Niño (NOAA, 2018). In this sense, several studies have shown that abrupt climatic variations lead to large population fluctuations of insects, including Lepidoptera (Woiwod, 1997; Cornelissen, 2011; Wilson and Maclean, 2011). In addition to the annual oscillations, one should pay attention to the monthly variations in precipitation (Fig. 2) because it varied considerably in the same crop season from one month to another, and in the same month in the different crop seasons, consequently influencing the other monthly meteorological factors differently. The result of this is that insect populations that have a relatively short life cycle were subjected to great climatic variations either directly or indirectly associated with the availability of host plants.

The significant correlation between meteorological factors and ONI with the specific abundance of the three species (Table 3) indicate that the direct relationship of the oscillation of ONI with cyclical climatic variations (Holmgren et al., 2001) including episodes of drought at the studied site (Figs. 2 and 3), can be used to make predictions and proactive management of pests. To make more precise predictions, however, long-term studies in different places and monitoring both adult and immature forms are necessary (Summerville and Marquis, 2017). Beyond that, the different characteristics of the species and agroecosystems need to be considered, including dispersion capacity (Ferguson et al., 1991), the effects of the agricultural landscape on metapopulations (Mennechez et al., 2003; Colombo and Anteneodo, 2015), gene exchanges (Nagoshi et al., 2017), natural biological control (Pereira et al., 2018), phytosanitary products and cultural practices (Gallo et al., 2002).

The relationship (despite seasonal differences) of the population dynamics of *A. infecta*, *E. agrotina* and *S. frugiperda* with meteorological variables and ENSO indicate the possibility of forecasting related to increases or even population outbreaks, subsidize decision-making to their management. In order to increase the precision of the models associated to the forecasts, it is necessary to monitor these insects for a longer period, including more climatic variations episodes, especially the related to El Niño and La Niña events.

Conflicts of interest

The authors declare no conflicts of interest.

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