



# The role of natural enemies in regulating the population of the outbreak species *Orgyia trigotephras* (Lepidoptera: Erebidae) in North Africa

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## Abstract

The outbreak species, *Orgyia trigotephras* caused significant defoliation in northeastern Tunisia in 2005. This work aims to elucidate the population cycle of this pest by testing a wide range of variation of fecundity and population growth. The recorded fecundity was at its highest peak with an average of 153 eggs/egg batch during outbreaks. The action of the complex of egg parasitoid/predator associated with *O. trigotephras* varies over time. The action of *Aprostocetus* sp. and *Coccidiphila rungsella* was at its utmost during the collapse phase of the insect in 2007 and 2014. Only these two species were recorded over our 17-year study. A low proportion of dried eggs versus a high proportion of unfertilized eggs were observed due to the poor quality of foliage consumed by the mother larva during its development. The correlation between fecundity and unfertilized eggs was highly significant. Fecundity change indicators of *O. trigotephras* are indirect, namely defoliation by high densities of larvae reducing leaf quality for the next generation. The abundance of the host species makes it easily found by parasitoids or vulnerable to parasitism. This strategy is used by *O. trigotephras* since the action of natural enemies is very low. Yet, the insect was not observed since 2018. It will be important to conduct large research in the region to see whether the insect is still present in the localities or relocate to other ones near the studied site.

**Keywords** *Aprostocetus* sp. · *Coccidiphila rungsella* · Eggs mortality · Fecundity · Tunisia

## Introduction

Population cycles are determined by biotic/abiotic or by intrinsic/extrinsic factors (Elton 1927; Rossiter 1994; Myers and Cory 2013). Natural enemies are reported as the main driving force in limiting and regulating the pest insect (Münster-Swendsen 1985; Berryman 1996; Wyckhuys and O'Neil 2006), suppressing incipient outbreaks and limiting the spatial spread of existing outbreaks (Maron et al. 2001; Maron and Harrison 1997). Along with multispecies

models involving mixes of parasitoids, predators, and pathogens (May and Hassell 1988), other researchers believe that parasitoids do not cause sufficient mortality to limit the growth of populations (Campbell et al. 1977; Ticehurst et al. 1978). Forest structure may also affect the parasitism rates and survival of forest defoliators (Cappuccino et al. 1998). Likewise, maternal effects (e.g. development rate and final size of offspring) are related to egg size and the order of laying (Rossiter 1994). Long-time series studies on outbreak pests were mostly conducted on larval parasitoids (Münster-Swendsen 1985; Montgomery and Wallner 1988). The goal of this research is to identify factors responsible for maintaining the population dynamic of the outbreak pest, *O. trigotephras* at low densities at the egg stage. This negative density-dependent could explain the decline of population on the following years. This Erebidae caused significant defoliation of maquis in northern Tunisia in 2005 (Ezzine et al. 2010) and on *Pistacia lentiscus* in Italy in 2010 (Bella et al. 2011). In this context, this work aims to elucidate the population cycle of *O. trigotephras* by testing (i) a wide range of variation of fecundity and population growth; (ii)

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the interaction between parasitism and predation of eggs of *O. trigotephras* and another intrinsic effect of eggs mortality as unfertilized and eggs containing dead larva by measuring long-term average levels (population abundance) from 2005 to 2021.

## Materials and methods

### Sampling

Investigations were carried out in northeastern Tunisia (36°849'N; 10°779'; alt. 410 m), in the forest of Jebel Beni Oulid (2670 ha) from 2005 to 2021. The region is under a sub-humid climate with a warm winter, characterized by Mediterranean vegetation, mainly the cork oak series represented by the *Quercus coccifera*, *Erica arborea*, and *Lavandula stoechas* group. Average annual rainfall varies between 450 mm and more than 600 mm (DGF 1995).

Females of *O. trigotephras* lay eggs in late May-early June. Egg batches can be oviposited in leaves of evergreen plants, namely *Callicotome villosa*, *Erica arborea*, *E. multiflora*, and *Phillyrea media*, and mainly on *Quercus coccifera* and *Pistacia lentiscus* (Ezzine 2016). Thereby, egg batches ( $n \leq 30$ ) were firstly collected on *P. lentiscus* from 2005 to 2015. Since 2016, egg batches were only observed on *Q. coccifera* on which we collected the detected ones. Once in the laboratory, these latter were kept individually in plastic boxes at ambient temperature ( $25 \pm 2$  °C) until the emergence of natural enemies (Ezzine et al. 2010, 2015).

### Laboratory trials

As the eggs of *Orgyia trigotephras* are protected inside a cocoon, egg batches were rubbed with a stiff bristle brush against a strainer over a bowl. The mesh of the strainer is less than 1 mm (size of the egg) to retain eggs and let the bristle (Ezzine et al. 2010). Eggs were then placed in a petri dish (9 cm  $\varnothing$ ) and observed under a binocular microscope to distinguish different types of eggs. Natural enemies were kept in the Eppendorf tube, in ethanol (96%), or killed with ether before morphological identification (Ezzine et al. 2015).

### Statistical analysis

Statistical analyses were performed using the SPSS-10.0 software package for Windows. The average number of eggs/egg batch (fecundity), parasitized, predated, “unfertilized, and dried eggs” were calculated and reported as mean  $\pm$  standard error of the mean (MSE). Differences in egg categories among years were tested with analysis of variance (ANOVA) followed by multiple comparisons of means using the Duncan test.

Dispersion index ( $DI = \text{Var}(X)/\text{Average}(X)$ ) values were estimated for both parasitized and predated egg numbers. The correlation between predated and parasitized eggs was calculated using the Pearson correlation coefficient.

## Results

### Egg categories

Sorting eggs allowed us to identify five types of eggs; (i) parasitized eggs present a circular and regular exit hole. The interior emptied contains often waste black (rest of larva); (ii) predated eggs, in general, are fragments derived chorions eggs predation; (iii) dried eggs are mostly flat, “brown, black or orange”, and contain a dry larva; (iv) flattened eggs are unfertilized; and (v) hatched eggs recognizable through the large and reniform or circular exit hole of the larva.

### Female fecundity

The number of eggs/egg batches (fecundity) varied significantly among years (ANOVA,  $F_{(16, 314)} = 15.768$ ,  $P < 0.001$ ). In 2005 and 2014, fecundity was higher on average (153 eggs/egg batch). It was lower in 2007 with an average of  $45 \pm 5.63$  eggs/egg batch. Yet, for the other years, the fecundity average varied between 60 (2017) and 133 (2015) eggs/egg batches (Fig. 1). The maximum number of eggs was 238 eggs (2010), however, the minimum was 5 eggs (2006).

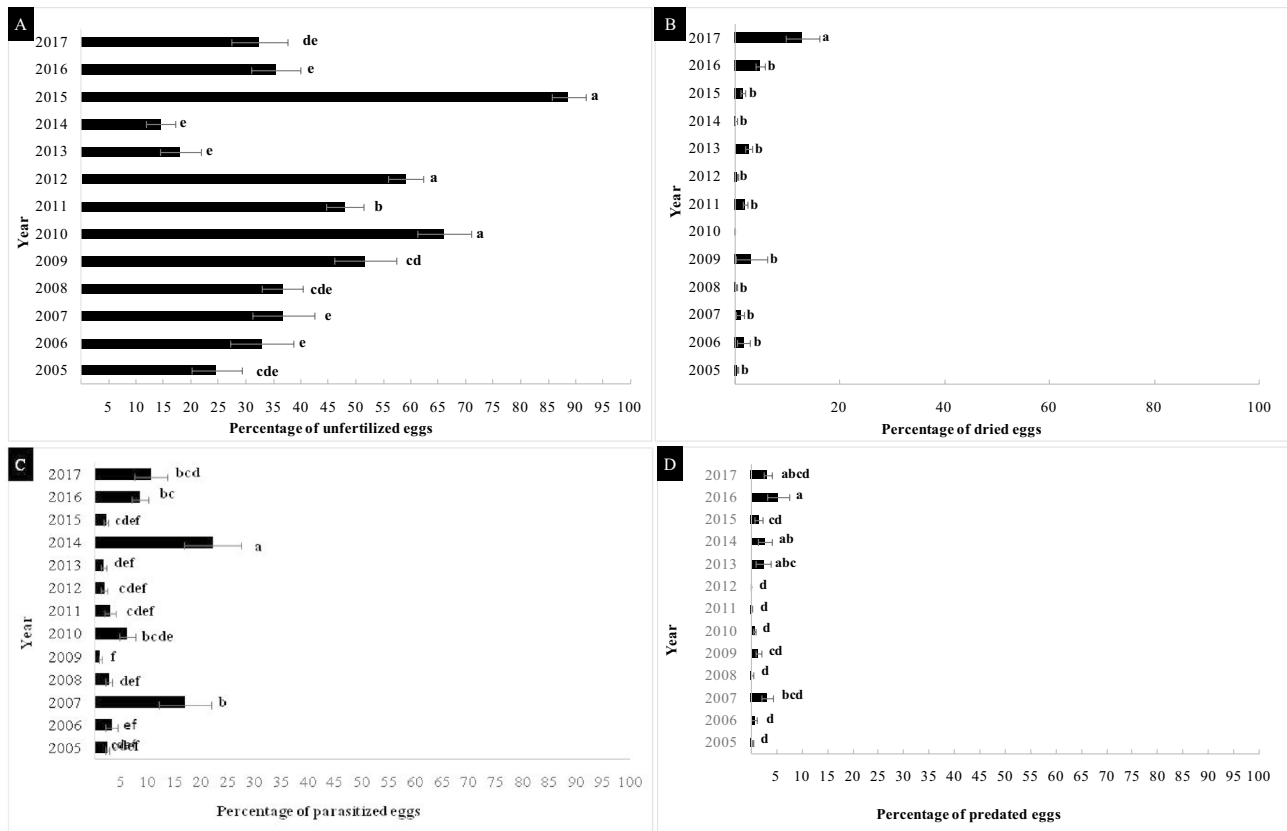
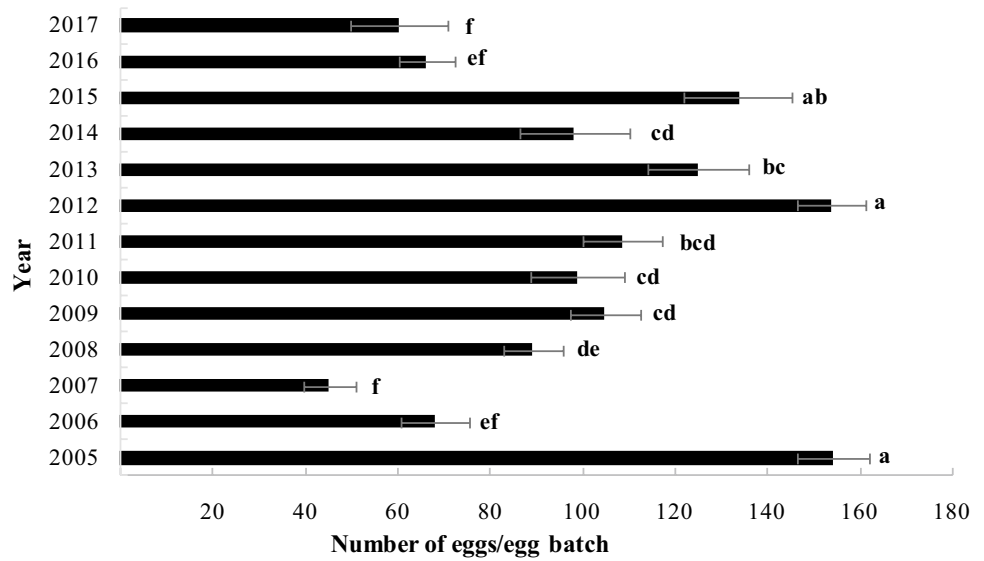
### Egg mortality

Egg mortality includes dried eggs, flattened/unfertilized eggs, “predated eggs, and parasitized eggs”. Percentage of each category varied significantly among years ( $P < 0.001$ ). According to multiple comparisons of means Duncan, six groups of unfertilized eggs were identified. In 2015, we recorded the highest mean percentage ( $88.73 \pm 3.07\%$ ) and the lowest in 2014 ( $14.43 \pm 2.6\%$ ) (Fig. 2A). The maximum percentage of unfertilized eggs was 100% (2005, 2006, 2008, and 2009), however, the minimum was 0.00% (2006, 2010, 2014, and 2017).

The highest mean percentage of dried eggs was recorded in 2017 ( $12.86 \pm 3.19\%$ ). It was lower than the other years and it does not exceed 4% (Fig. 2B). The maximum percentage of dried eggs was 90.43% (2009), however, the minimum was 0.00% throughout the study period.

One parasitoid, the Hymenoptera, Eulophid *Aprostocetus* sp. parasitized the eggs. Even, predation was caused by the larvae of the Cosmopterigidae, *Coccidiphila rungsella* Nel and Brusseau, 1997 (Ezzine et al. 2015). The mean percentage of parasitized eggs varied between  $1.08 \pm 0.25$  (2009) and  $22.09 \pm 5.4$  (2014) (Fig. 2C). The maximum was 72.27%

**Fig. 1** Female fecundity or Average number ( $\pm$  SE) of eggs/egg batch of *Orgyia trigotephras*. Within each year, values labeled with different superscript letters are significantly different (Duncan's Multiple Range test,  $P < 0.05$ )



**Fig. 2** Average percentage number ( $\pm$  SE) of unfertilized eggs (A), dried eggs (B), parasitized eggs (C), and predated eggs (D)/ egg batch of *Orgyia trigotephras*. Within each year, values labeled with different

superscript letters are significantly different (Duncan's Multiple Range test,  $P < 0.05$ )

and the minimum was 00%. On the other side, predation varied between 00% (2012) and  $5.33 \pm 2.16$  (2016) (Fig. 2D), with a maximum of 36.84% (2016).

The dispersion index (DI) was well above 1.0 in all studied years (except 2011 and 2012 for predated eggs). It shows

**Table 1** Average number ( $\pm$ SE) of parasitized and predated eggs (B)/egg batch of *Orgyia trigotephras*; and dispersion index values for the natural enemies (parasitoid and predator)

Year	Parasitized eggs		Predated eggs	
	Mean	DI	Mean	DI
2005	4 $\pm$ 0.68 <sup>cdef</sup>	3.5	0.33 $\pm$ 0.14 <sup>d</sup>	1.93
2006	1.66 $\pm$ 0.35 <sup>ef</sup>	2.24	0.1 $\pm$ 0.07 <sup>d</sup>	1.62
2007	7.3 $\pm$ 2.38 <sup>b</sup>	7.76	1.1 $\pm$ 0.37 <sup>bcd</sup>	1.3
2008	2.23 $\pm$ 0.47 <sup>def</sup>	3.01	0.1 $\pm$ 0.1 <sup>d</sup>	3
2009	1.1 $\pm$ 0.29 <sup>f</sup>	2.34	0.9 $\pm$ 0.22 <sup>cd</sup>	1.71
2010	4.4 $\pm$ .81 <sup>bcd</sup>	4.47	0.46 $\pm$ 0.17 <sup>d</sup>	1.88
2011	2.46 $\pm$ .97 <sup>cdef</sup>	11.59	0.1 $\pm$ 0.05 <sup>d</sup>	0.93
2012	2.43 $\pm$ 0.77 <sup>cdef</sup>	7.35	0 <sup>d</sup>	0
2013	2 $\pm$ .77 <sup>def</sup>	4.47	2.33 $\pm$ 1.33 <sup>abc</sup>	13.76
2014	14.85 $\pm$ 1.77 <sup>a</sup>	2.97	2.78 $\pm$ 1.52 <sup>ab</sup>	11.71
2015	2.66 $\pm$ 0.54 <sup>cdef</sup>	2.02	1.05 $\pm$ 0.39 <sup>cd</sup>	2.61
2016	5.57 $\pm$ 1.31 <sup>bc</sup>	8.06	2.96 $\pm$ 1.17 <sup>a</sup>	12.14
2017	5.08 $\pm$ 1.66 <sup>bcd</sup>	12.52	1.39 $\pm$ 0.25 <sup>abcd</sup>	1.09

For each column, values followed by the same letters are not significantly different based on Duncan's Multiple Range test at  $P < 0.05$

**Table 2** Correlation coefficients (R) between fecundity and types of eggs

Parameters	Parasitized eggs	Unfertilized eggs	Dried eggs	Predated eggs
Fecundity	0.030 <sup>ns</sup> (0.589)	0.588 <sup>**</sup> (0.000)	0.054 <sup>ns</sup> (0.339)	- 0.122 <sup>*</sup> (0.02)
Parasitized eggs		- 0.079 <sup>ns</sup> (0.159)	0.170 <sup>**</sup> (0.002)	0.125 <sup>*</sup> (0.02)
Unfertilized eggs	- 0.079 <sup>ns</sup> (0.159)		- 0.037 <sup>ns</sup> (0.507)	- 0.143 <sup>*</sup> (0.01)
Predated eggs	0.125 <sup>*</sup> (0.02)	- 0.143 <sup>*</sup> (0.01)	0.064 <sup>ns</sup> (0.252)	

P: the asymptotic significance. ns: not significant ( $P > 0.05$ ); \*: significant ( $0.01 < P < 0.05$ ); \*\*: highly significant ( $P < 0.01$ ). P values are in parentheses

the gathering distribution of parasitoid and predator attacks (Table 1).

The number of parasitized or dried eggs was not significantly correlated with Fecundity. Yet, the number of unfertilized or predated eggs was significantly correlated with fecundity. On the other hand, parasitized eggs were significantly correlated with dried and predated eggs. Unfertilized eggs were significantly correlated with predated eggs. Parasitized and predated eggs were correlated significantly (Table 2).

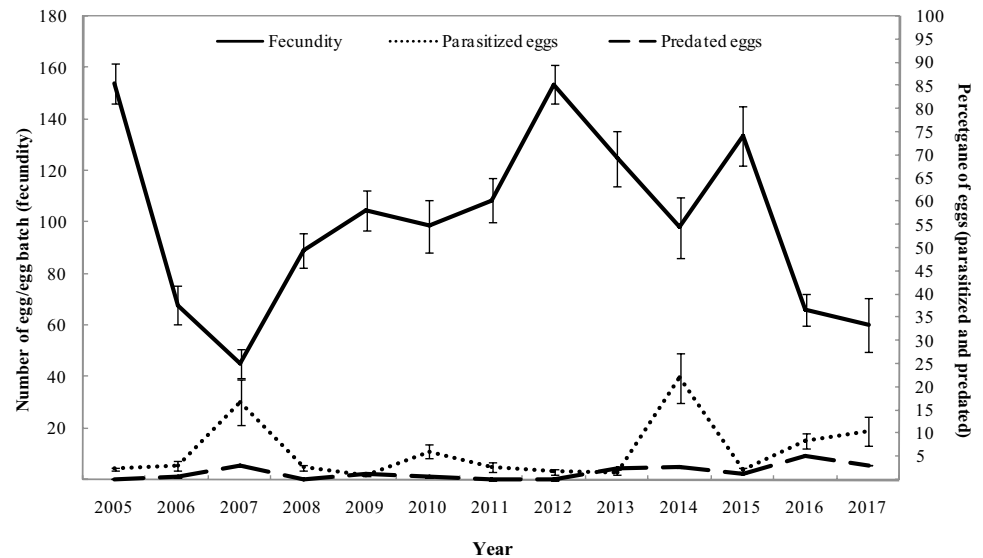
Figure 3 shows the simulation between fecundity, parasitized, and predated eggs. Two highest peaks of fecundity ( $> 153$  eggs/egg batch) were observed in 2005 and 2012, and a relatively low one in 2015 (134 eggs). The highest peak of parasitism was observed in 2014 (22%) and a relatively low one in 2007 (16%). The same results were observed for predation, a peak in 2016 (5.33%) and two relatively low ones in 2013 (2.41%) and 2014 (2.78%).

## Discussion and conclusion

Given the long-term available data sets, we studied the female fecundity and the mortality factors of eggs of *O. trigotephras* and the action of natural enemies. Like other

outbreak insects, *O. trigotephras* occurs in many sites at low densities, and a few sites at very high densities (Harrison 1997; Maron et al. 2001; Ben Jamâa et al. 2002; Ezzine et al. 2021). In 2005, the first year of a large outbreak (progradation phase), larvae density of *O. trigotephras* was very high and larvae fed on *Quercus coccifera*, *Pistacia lentiscus*, *Callicotome villosa*, *Erica arborea*, *E. multiflora*, *Arbutus unedo* and *Cistus Crispus* (Ezzine et al. 2010; Ezzine, 2016). The recorded fecundity was at its highest peak with an average of 153 eggs/egg batch (max = 232 eggs). From 2006 to 2012, the insect was present but with a low density (latency phase). In 2012, a second and low outbreak was observed with female fecundity of 153 eggs/ egg batch (max = 227 eggs). During these years, the density of *O. trigotephras* was very low and it correspond to the retro gradation phase of the insect till 2018 wherein no more egg batch was observed on any host plant in this site. According to Myers

**Fig. 3** Average number ( $\pm$  SE) of eggs per egg batch, percentage of parasitized eggs, and predated eggs of *Orgyia trigotephras*



and Cory (2013), three factors are required for cyclic population dynamics: the first one is a high fecundity to allow the population to increase by three to six orders of magnitude during the four or five generations of the increase phase; the second one is the density-related, increased mortality factors initiating the decline at peak density; and the last one is delayed density-related mechanisms inducing the decline of the population. A review of Berryman (1996) on cyclic forest Lepidoptera led to conclude that parasitoids invariably kill a consistently high proportion of lepidopteran eggs, larvae, and pupae during the decline phase and relax their effects during the increase phase. According to the data reported in the present paper, the action of the complex of egg parasitoid/predator associated with *O. trigotephras* varies in time. The action of *Aprostocetus* sp. and *C. rungsella* was at its utmost during the collapse phase of the insect in 2007 and 2014. Only very low numbers of *Aprostocetus* sp. were recovered from *O. trigotephras* moth eggs and were found to cause a lower percentage of parasitism and did not exceed 22% (2014). Yet, predation caused by larvae of *C. rungsella* was very low and the percentage did not exceed 5% (2016). Only these two species were recorded over our 17-year study. The deepest study conducted by Myers and Cory (2013) showed that parasitism is a universal mortality factor for forest Lepidoptera. Parasitism by hymenopteran parasitoids leads to a delayed density dependence capable of producing cyclic oscillations in the population dynamics of Lepidoptera (Berryman 1996; Tanhuanpää et al. 2002). Egg parasitism of *L. dispar* was unimportant as a mortality factor in the examined Slovak populations compared to the other stages (Hoch et al. 2001). The Eulophid parasitoids were reported to be successfully used to control important forest pests (Voegelé 1989; Duan et al. 2013; Wang et al. 2021). Generally, parasitoids parasitize fertilized host eggs

(Krugner 2014) since it's important for parasitism and fitness of the parasitoid offspring (Wang et al. 2020). *Aprostocetus* spp. were used in forestry to control pests (Sampson et al. 2013) and, parasitize the eggs of Lepidoptera (Yang et al. 2015). In Viggiani (2021), it was reported that egg parasitoids, *Aprostocetus*, *Anastatus bifasciatus*, and *Baryscapus* sp. of *Phaneroptera nana*, oviposit in the host eggs in autumn and complete a generation in the next spring–summer and can also develop another generation on the same host in summer–autumn. Our results showed that the biology of *Aprostocetus* is synchronized with the egg deposition of *O. trigotephras*. On the other side, females of other species, as the trichogrammatid oviposit in the host egg in autumn and a long development takes place (Viggiani 2021). Ezzine et al. (2020) elucidate the effect of pupa parasitoids on the outbreak species the Erebidae, *Casama innotata* which suggests the existence of strong natural regulation mechanisms, by the mortality of more than 93% of the population by parasitoids. In our work, results indicate that natural enemies play a role in maintaining this population dynamic but with a low proportion. Nevertheless, intrinsic factors may play a crucial role in regulating the population. Our findings showed a low proportion of unfertilized eggs (< 13%). Contrariwise, the proportion of unfertilized eggs was very important and ranged between 15% (2014) and 89% (2015). These defective eggs do not have a complete plan for building an embryo or being incapable of further development. This may be due to the poor quality of foliage consumed by the mother larva during its development (Ezzine et al. 2010, 2015). The correlation between fecundity and unfertilized eggs was highly significant. Fecundity change indicators of *O. trigotephras* are indirect, namely defoliation by high densities of larvae reducing leaf quality for the next generation (Ezzine et al. 2015). Furthermore, Villemant and Fraval



(1992), considered that after strong defoliation caused by *Lymantria dispar*, the attack of the parasitoid was low and it was due to the high proportion of dry eggs resulting from the poor nutrition of parents.

The abundance of the host species makes it easily found by parasitoids or vulnerable to parasitism. Thus, existence at relatively low abundance may provide refuge from parasitism (Barbosa 2004). Maybe, this strategy is used by *O. trigotephras* since the action of natural enemies is very low. Yet, the insect was not observed since 2018, it's probably due to the competition that reigns in the studied site since 2013 (Hammami et al. 2019). It will be important to conduct large research in the region to see whether the insect is still present in the localities or relocate to other ones near the studied site.

To conclude, biological control involves the mutualism among natural enemies affecting the same host (May and Hassell 1988). The broad objective of this study is to look for biological control as it reduces the average abundance of a pest by using one or more populations of natural enemies, and in so doing reduce insect outbreaks. These results caution us against formulating biological control strategies purely in terms of two-species systems. The cyclic dynamics can be affected by environmental disturbances. It's so important to emphasize other ways for future studies to expand cyclic population dynamics mechanisms, considering the effect of climate change and phenology in elucidating patterns of synchrony among populations and outbreaks.

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**Data availability** We admit that the results in the paper will be archived in an appropriate public repository.

## Declarations

**Conflict of interest** The authors have no competing interests to declare that are relevant to the content of this article.

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