Zoology and Ecology, 2025, Volume 35, Number 2
Online ISSN: 2165-8013
https://doi.org/10.35513/21658005.2025.2.2

COMPARATIVE ANALYSIS OF EGG BATCH CHARACTERISTICS, BRANCH PREFERENCES, HATCHING RATES, AND PARASITISM IN *THAUMETOPOEA BONJEANI* AND *THAUMETOPOEA PITYOCAMPA*

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Djeddai, R., Rahim, N., Mahdi, Kh. 2025. Comparative analysis of egg batch characteristics, branch preferences, hatching rates, and parasitism in *Thaumetopoea bonjeani* and *Thaumetopoea pityocampa*. *Zoology and Ecology* 35(2), 101–114. https://doi.org/10.35513/21658005.2025.2.2

Article history:
Received 26 January 2025,
accepted: 08 August 2025

Keywords: *Thaumetopoea pityocampa*; *Thaumetopoea bonjeani*; *Cedrus atlantica*; fecundity; egg mortality; parasitism; Algeria

Abstract. In Algeria, two *Thaumetopoea* species (Lepidoptera: Notodontidae), *Thaumetopoea bonjeani* (cedar processionary moth, CPM) and *Thaumetopoea pityocampa* (pine processionary moth, PPM), coexist in *Cedrus atlantica* forests causing significant tree damage and posing health risks to humans. This study investigates key bioecological differences between these species, which share similar environmental conditions, by comparing their reproductive potential, with a focus on fecundity, egg batch characteristics, and mortality factors. A total of 125 egg batches were collected from *C. atlantica* in two cedar forests: 75 batches of *T. pityocampa* were collected from Chréa forest and 50 batches of *T. bonjeani* from Tala-Guilef forest. The PPM showed significantly higher fecundity, with an average of 222.68 eggs per egg batch, compared with 135.84 eggs for CPM. Although mean egg batch lengths were similar (~25 mm), PPM females preferred larger branches (2–10 mm diameter) than CPM (2–7 mm). The average number of egg rows per batch was greater in PPM (10.77) than CPM (5.56). Regression analysis revealed positive correlations between egg batch length, egg count, and row number in both species, although branch diameter was significantly correlated only in CPM. Hatching rates were higher for PPM (90.6%) compared to CPM (60.4%), with predation being the primary mortality factor for CPM eggs (17.1%) compared to 1.1% in PPM. Egg parasitism also differed significantly between the species, with *Ooencyrtus pityocampae* dominating CPM parasitism and *Baryscapus servadeii* and *Trichogramma* sp. predominating in PPM. These findings enhance our understanding of species-specific life-history strategies and offer important implications for the development of targeted and ecologically informed pest management approaches in Mediterranean forest ecosystems.

INTRODUCTION

The genus *Thaumetopoea* includes species recognized as significant forest defoliators (Roques 2015). Within this genus, two groups of processionary moths are associated to conifers, the summer and winter processionary moths. The summer species develop in spring and early summer, while the winter species remain active during autumn and winter (Démolin 1988; Basso et al. 2016). These species cause substantial economic damage and pose serious health risks to both humans and animals due to their urticating setae, microscopic hairs that develop from the third instar onward in the larvae and can trigger severe allergic reactions and contact dermatitis (Battisti et al. 2024).

In Algeria, two species of processionary moths are known: the pine processionary moth (PPM) *Thaumetopoea pityocampa* (Denis and Schiffermüller 1775) and the cedar processionary moth (CPM) *Thaumetopoea bonjeani* (Powell 1922). The PPM is classified within the "winter group" and feeds on both *Cedrus* and *Pinus* species (Masutti and Battisti 1990; Démolin et al. 1994; Rahim 2025). It typically exhibits an annual life cycle (Battisti et al. 2015). Its life cycle comprises an aerial phase (adult, egg, larvae) and a hypogeal phase (pupa).

Under optimal conditions, development lasts about six months, although the duration of larval instars and pupation may be extended by winter conditions and diapause. Adult emergence occurs in July and lasts less than one month in populations with high density. Females lay between 70 and 300 eggs on pine needles or cedar branches. After 30–45 days, larvae hatch, form colonies, and display gregarious behaviour throughout their development. The larval development consists of five instars occurring during autumn and winter (Battisti et al. 2015). From the third instar onwards, larvae construct silken nests that create a favourable microclimate for overwintering (Rossi et al. 2025). In late winter, when the temperatures range from 10 and 22°C, fifth-instar larvae descend in procession toward the soil to pupate. In Algeria, pupation typically lasts from mid-February to late July. Some pupae may enter an extended diapause, remaining dormant in the soil for up to six years (Zamoum 1998). Consequently, adult emergence may be delayed for one or more years depending on environmental conditions. In Algeria, PPM populations exhibit cyclic outbreaks every 5–6 years, often leading to severe defoliation of pine and cedar stands (Sbabdji et al. 2015; Bouzar-Essaidi et al. 2023).

In contrast to the PPM (*T. pityocampa*), the CPM (*T. bonjeani*) belongs to the “summer group” of *Thaumetopoea* species. It feeds exclusively on *C. atlantica* and is endemic to high-altitude cedar forests in Algeria and Morocco (Démolin 1988). The CPM completes a univoltine life cycle (Rahim 2016). Oviposition occurs from August to September, with females depositing their eggs on the underside of small cedar twigs. These egg batches contain between 44 and 340 eggs (Gachi et al. 1986). Embryonic development extends over 50 days, after which the neonate larvae enter a winter diapause. The eggs hibernate for nearly 8 months and hatch in the following spring, between late March and late April, in synchrony with the vegetative growth of *C. atlantica*, thereby maximizing larval feeding success and survival. This precise phenological alignment contributes to CPM being regarded as the most damaging pest of *C. atlantica* in Algeria (Gachi et al. 2005; Rahim 2016). Throughout their development, CPM larvae exhibit pronounced gregarious behaviour. However, unlike *T. pityocampa*, they do not construct dense silk nests. The larval stage includes five instars, with the final instars causing the most severe defoliation of cedar foliage. Processions of fifth-instar larvae toward pupation sites begin in June or July, when ambient temperatures reach approximately 20 °C. Pupation occurs at shallow depths, and adult emergence takes place in late summer, between August and mid-September (Rahim 2016).

Both species lay their eggs in clusters under cedar branches camouflaging them with scales (Battisti et al. 2015). The homochromy of the scales with the branch colour is a protective strategy, making egg detection difficult (Gachi et al. 1986; Zamoum et al. 2017). The number of eggs in each cluster reflects the females fecundity, as both species lay all their eggs in a single batch (Battisti et al. 2015). Fecundity is influenced not only by the inherent fecundity potential to each species but also by various ecological factors (Chew and Robbins 1984). In Lepidoptera, the selection of an oviposition site is crucial, relying on a combination of chemical, physical and ecological characteristics of the host plant (Renwick and Chew 1994). Females ensure to select the most favourable sites to enhance the survival and success of their progeny (Thompson and Pellmyr 1991).

In some Algerian cedar stands, PPM and CPM coexist, sharing natural enemies like predators and parasitoids, which play an important role in the regulation of the two hosts populations (Zamoum et al. 2017). Three oophagous parasitoid species have been identified as common to both species in Algerian cedar forests: *Ooencyrtus pityocampae*, *Baryscapus servadeii* and *Trichogramma embryophagum* (Rahim et al. 2016; Zamoum et al. 2017; Ayache et al. 2021; Messaadia et al. 2021; Sebti et al. 2022).

The PPM has been the subject of several studies and is considered the most studied species within the genus *Thaumetopoea* (Basso et al. 2023). In contrast, limited research has focused on the CPM, with studies addressing its bioecology (Gachi et al. 1986; Démolin 1988; El-Yousfi 1989; Rahim 2016), fecundity (El Mokhefi et al. 2021) and parasitoid activity (Rahim et al. 2016; Zamoum et al. 2017). However, knowledge about the bionomics of CPM, particularly during the egg stage, remains scarce. Moreover, no comparative studies have investigated the fecundity or oviposition strategies of CPM and PPM females on the same host plant.

This study aimed to provide a revised interpretation of the bioecological differences between the cedar processionary moth (CPM) and the pine processionary moth (PPM), using an ecological, functional, and evolutionary approach. Specifically, it focused on: (1) comparing the characteristics of egg batches of these two species, which have different phenological life cycles, on the same host plant (*Cedrus atlantica*) in two Algerian cedar forests (Chréa and Tala-Guilef in the Djurdjura range), under similar altitudinal and climatic conditions, (2) analysing the oviposition strategies and preferences of females, and (3) evaluating egg mortality factors and parasitoid activity in both species.

MATERIALS AND METHODS

Study sites

The egg batches of *T. bonjeani* (CPM) and *T. pityocampa* (PPM) were collected from two natural stands of *C. atlantica* Manetti in northern Algeria, namely Tala-

Guilef and Chréa forests, where both species coexist (Rahim 2016; Rahim et al. 2021). The distance between the two sites is approximately 110 km. Tala-Guilef forest is located in Djurdjura National Park (latitude 36°47´N and longitude 4°00´E), at an elevation ranging from1400 to 1800 m. This area is characterized by a sub-humid climate, with annual precipitation reaching up to 1500 mm. The forest covers 200 hectares of *C. atlantica* stands with trees aged between 20 and 150 years. Situated about 86 km southeast of the capital Algiers, this site is primarily occupied by the summer processionary moth, *T. bonjeani*. Only one study has been conducted in this forest stand on the natural enemies of *Thaumetopoea bonjeani*, by Rahim et al. (2016), during a period when the pest exhibited a high population density and caused severe defoliation, leading to cedar tree dieback.

The second site, Chréa forest, is located in Chréa National Park on the Blidean Atlas massif (latitude 36°26´N and longitude 2°53´E) at elevations between 1000 and 1600 m. It is approximately 50 km southwest of Algiers. Above 1300 m, the forest is almost monospecific with cedar trees (Meddour 1994). The climate is classified as sub-humid, with annual precipitation ranging from 950 to 1200 mm. This park encompasses 1200 hectares of cedar forest. The structure of the forest is homogenous with a high density. The age of trees is between 80 to 120 years (Sbabdji et al. 2015). This site is predominantly occupied by the pine processionary moth, *T. pityocampa* (Sebti et al. 2022).

Sampling and laboratory rearing

A total of 125 egg batches were collected from the two forest sites at altitudes ranging from 1400 to 1600 m. In the Chréa forest, 75 egg batches of *T. pityocampa* were collected in August 2019, before larval hatching; from an altitudinal range of 1450–1550 m. Larval hatching in the egg batches sampled was observed at the beginning of August. In the Tala-Guilef forest, 50 egg batches of *T. bonjeani* were collected from cedar stands located at an altitude of 1500–1600 m. Due to the low infestation levels and the difficulty in locating the *T. bonjeani* egg batches in the field, the sampling at Tala-Guilef was conducted in two different periods. The first collection was performed in September 2019, during which 11 egg batches were obtained before larval hatching. The second period of sampling was in April 2020, resulting in the collection of 39 egg batches after hatching. Larval hatching in this site was observed in late March. For both species, all collected egg batches were laid during 2019.

The samples consisting of egg batches of the two species, associated with approximately 5 cm long branches of *C. atlantica* were collected (Figure 1). After collection, the egg batches were individually placed in test tubes sealed with cotton stoppers and transported to the Entomology Laboratory at Bouira university, where they were maintained at 22 ± 2 °C. Parasitoids emerging from the eggs were monitored daily, counted, removed from the test tubes, and transferred to smaller tubes for identification. This was done throughout the whole emergence period. After the end of the parasitoid emergence, the scales covering the egg batches were carefully removed using adhesive tape to facilitate accurate egg counting.

Biological material analysis

Branch diameters and egg batch lengths were measured using a calliper to determine the oviposition preferences and choices of each female species. Following these measurements, the egg batches were examined under a Wild stereo- microscope at 40× magnification to determine the number of eggs per batch and the different egg categories. Eggs were classified into one of the following five categories:

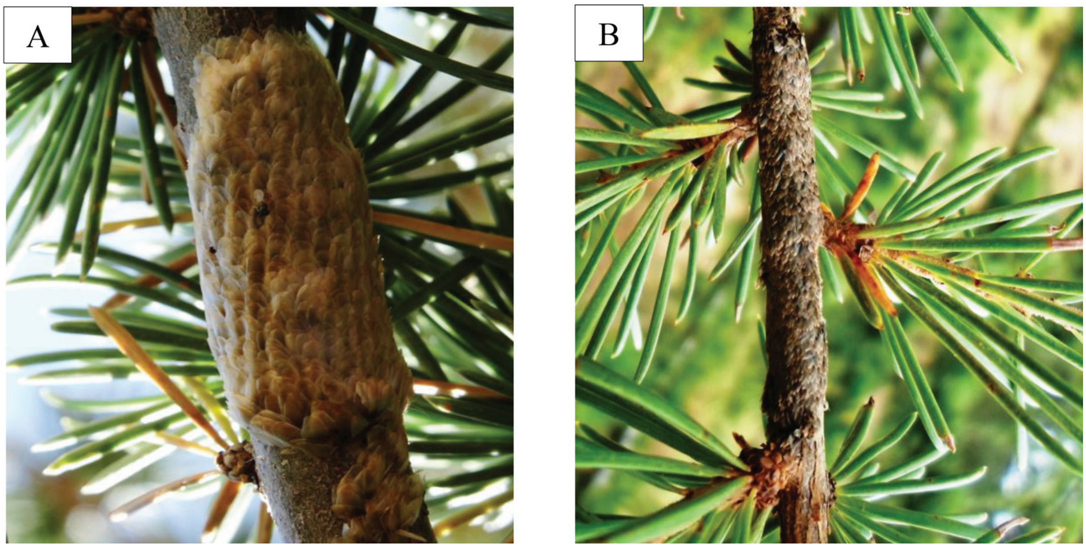

Figure 1. Egg batches of *T. pityocampa* (A) and *T. bonjeani* (B) collected from two forest stands: Chréa and Tala-Guilef.

- Hatched eggs: Identified by a large and whitish hole.
- Unhatched eggs: Eggs without any holes.
- Hatched eggs with dead larvae in it: Containing larvae that did not survive.
- Predated eggs: Eggs that were consumed by predators.
- Parasitised eggs: Presence of emergence holes of parasitoids.

The eggs without a hole in the shell and the parasitised eggs were completely dissected and the meconia and remains of dead and emerged parasitoids were determined according to Schmidt and Kitt (1994) and Tanzen and Schmidt (1995). According to these authors, the meconium of *Ooencyrtus pityocampae* is a yellow flat disc shaped, while that of *Baryscapus servadeii* appears as a single ball attached to the shell. The emergence of *Trichogramma* sp. was easily recognized by the presence of smaller round holes in the eggshell (Figure 2) (Schmidt and Douma-Petridou 1989).

Statistical analysis

One-way ANOVA was conducted to estimate differences in the egg batch characteristics and the global parasitism rates between the two species, after assessing for normality and homoscedasticity of the data. Normality and homoscedasticity were evaluated using the Shapiro-Wilk test. Data that did not follow a normal distribution ($p < 0.05$) were transformed to normalize the distributions, thereby allowing the application of parametric ANOVA.

The mean egg diameter was estimated indirectly from an egg batch factor (F), defined as the number of eggs divided by the product of the number of rows and the egg batch length, using the method described by Schmidt et al. (1999):

$$F = \text{number of eggs} / (\text{number of rows} \times \text{egg batch length}).$$

Since the eggs are laid without any visible space between them, their average diameter can be approximated by the inverse of this factor (1/F).

To assess the relationship among egg batches lengths, branch diameters, number of rows, and the number of eggs per batch, linear regression analyses were conducted.

The global parasitism rate was defined as the ratio between the number of parasitised eggs and the total number of eggs observed in each population. For statistical purposes, a parasitism rate per egg batch presented as the ratio between the number of parasitised eggs per egg batch and the total number of eggs in the egg batch was also calculated, treating each egg batch as an independent statistical unit.

Comparisons of parasitism rates between PPM and CPM egg batches were conducted using the Mann–Whitney U test. Each egg batch was considered as a statistical unit in these comparisons. All statistical analyses were carried out using SPSS software version 26.0 (IBM Corp., Armonk, NY USA). Statistical significance was set at $p < 0.05$.

RESULTS

Comparison of egg batch characteristics and branch selection preferences in *T. bonjeani* (CPM) and *T. pityocampa* (PPM)

The biometrics of the supporting branches and egg batch characteristics for CPM and PPM are summarized in Table 1.

The results showed a significant difference in the number of eggs laid by females of the two species on the cedar branches (one-way ANOVA, $F = 85.84$,

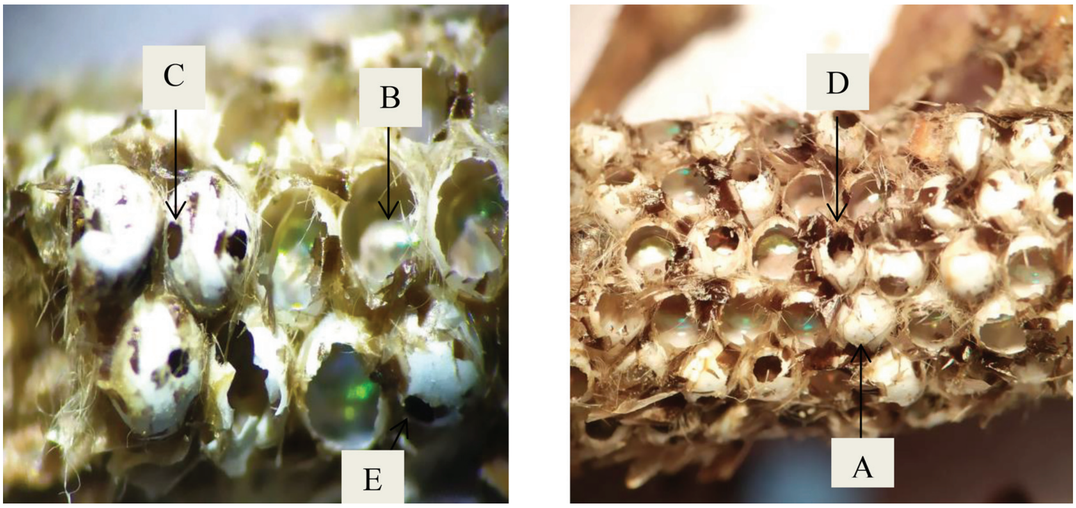

Figure 2. Egg categories observed in *T. pityocampa* and *T. bonjeani* batches: (A) unhatched egg, (B) emergence hole of processionary moth larva, and Hymenopteran parasitoids (C, D, E) *Trichogramma* sp. (C), *O. pityocampae* (D), and *B. servadeii* (E).

Table 1. Comparison of egg batch characteristics between *T. bonjeani* (CPM) and *T. pityocampa* (PPM).

Species	*T. bonjeani* (CPM)	*T. pityocampa* (PPM)	*F*	*P*
Sample size	50	75		
Variables	Mean ± SD (min–max)	Mean ± SD (min–max)		
Number of eggs per batch	135.84 ± 43.80 (37–238)	222.68 ± 55.77 (72–354)	85.84	0.000
Egg batch length (mm)	25.58 ± 7.22 (9–50)	25.25 ± 6.23 (13–44)	0.07	0.790
Branch diameter (mm)	3.22 ± 0.14 (2–7)	3.71 ± 1.51 (2–10)	3.97	0.049
Rows number	5.56 ± 1.20 (3–8)	10.77 ± 2.50 (4–17)	188.0	0.000
Egg diameter (mm)	1.04 ± 0.14(0.7 –1.29)	1.10 ± 0.13 (0.81–1.3)	7.490	0.007

$p < 0.001$). PPM exhibited higher fecundity than CPM, with the number of eggs per batch ranging from 37 to 238 (mean: 135.84) for CPM and from 72 to 354 (mean: 222.68) for PPM. However, no significant difference was observed in the average length of the egg batches between the two species, with both exhibiting nearly identical mean values of approximately 25 mm (one-way ANOVA, $F = 0.07$, $p = 0.790$). The estimated egg diameters of PPM and CPM, calculated using the F factor, revealed a significant difference between the two species (one-way ANOVA, $F = 7.490$, $p < 0.05$). PPM eggs demonstrated a larger mean diameter (1.1 mm) compared to those of CPM (1.04 mm).

Branches selected for egg deposition by PPM females ranged in diameter from 2 to 10 mm, while those chosen by CPM ranged from 2 and 7 mm, indicating the preference by PPM for larger branches (one-way ANOVA, $F = 3.97$, $p < 0.05$). Furthermore, a comparison of the number of rows per egg batch revealed a highly significant difference between the two species (one-way ANOVA, $F = 188$, $p < 0.001$), with PPM egg batches exhibiting higher mean values (10.77) compared to CPM (5.56).

Relationships between total egg number, egg batch length, row number, and branch diameter

The linear regression analysis revealed a positive correlation ($p < 0.001$) between egg batch length and the total number of eggs in both CPM and PPM, with moderately low R^2 values of 0.232 for CPM and 0.262 for PPM (Figure 3). Similarly, a positive correlation ($p = 0.003$ for CPM and $p = 0.002$ for PPM) was found between the total number of eggs and the number of rows per egg batch, with R^2 values of 0.171 for CPM and 0.124 for PPM (Figure 4). A positive correlation ($p = 0.05$ for CPM) was also observed between the total number of eggs per batch and branch diameter, with low R^2 value of 0.151 for CPM. In contrast, no significant correlation was found for PPM ($p = 0.180$), with R^2 value close to zero (Figure 5).

Hatching rates and mortality factors between CPM and PPM egg batches

The hatching rate of larvae was higher in PPM (90.6%) compared to CPM (60.4%) (Figure 6). However, this difference was not statistically significant (one-way ANOVA, $F = 113.99$, $p = 0.126$) (Table 2). Mortality rates were considerably higher in CPM, accounting for almost 40% of the total eggs, compared to only 10% in the PPM. Predation was the main cause of mortality in CPM eggs, with a rate of 17.1%, compared to 1.1% in PPM eggs (Figure 6). Statistical analysis showed that this difference was highly significant ($F = 15.39$, $p < 0.001$) (Table 2). The impact of egg parasitoids was 3.3% and 7.2%, respectively, in PPM and CPM eggs. Unhatched eggs, either sterile or with incomplete embryo development, exhibited significantly higher

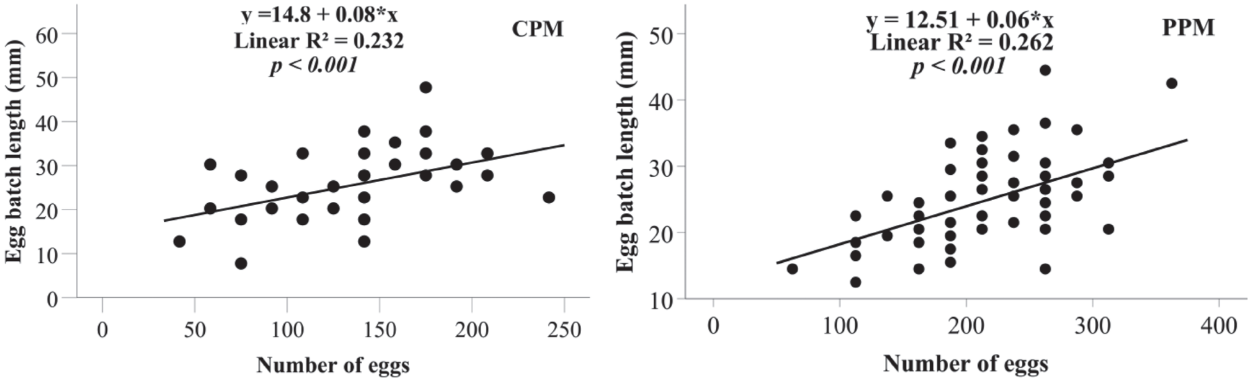

Figure 3. Correlation between egg batch length and the total number of eggs per batch in *T. bonjeani* (CPM) and *T. pityocampa* (PPM).

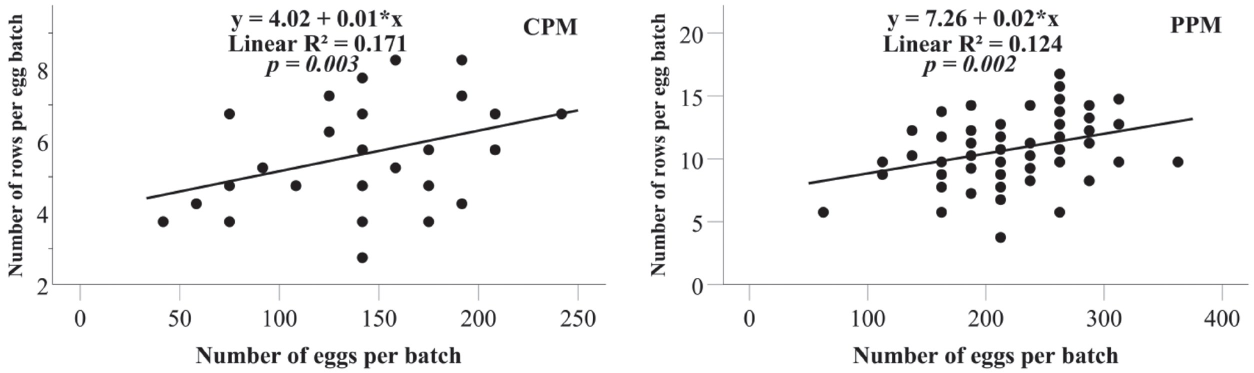

Figure 4. Correlation between the number of rows in egg batches and the total number of eggs per batch of *T. bonjeani* (CPM) and *T. pityocampa* (PPM).

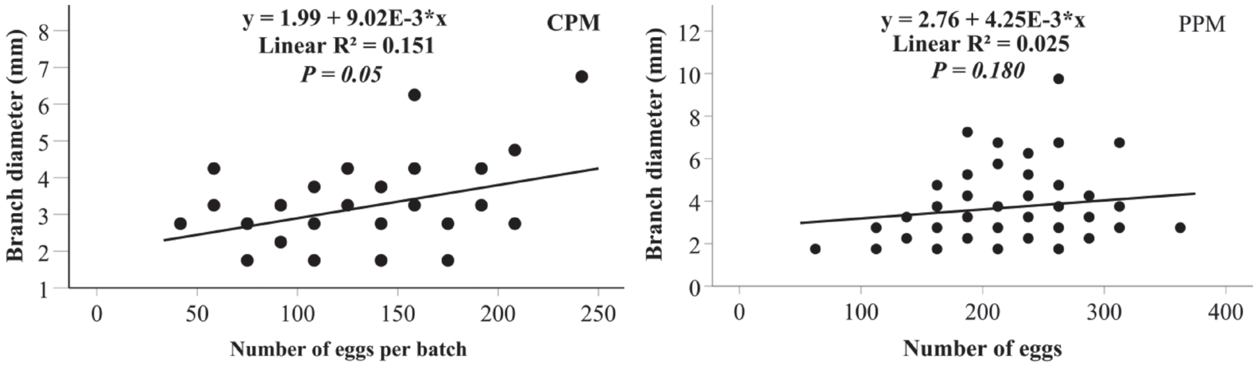

Figure 5. Correlation between branch diameter and the total number of eggs per batch in *T. bonjeani* (CPM) and *T. pityocampa* (PPM).

Table 2. Mean (± SD) number of larvae hatched and egg mortality in *T. bonjeani* (CPM) and *T. pityocampa* (PPM).

Species	*T. bonjeani* (CPM)	*T. pityocampa* (PPM)	*F*	*P*
Sample size	50	75		
Variables	Mean ± SD (min–max)	Mean ± SD (min–max)		
Larvae hatched	82.06 ± 54.91 (0–209)	201.84 ± 65.42 (21–344)	113.99	0.126
Unhatched eggs	16.78 ± 17.16 (0–66)	9.09 ± 13.30 (0–56)	7.93	0.006
Predated eggs	23.48 ± 43.04 (0–136)	2.47 ± 14.27 (0–110)	15.39	0.000
Parasitised eggs	9.72 ± 17.25 (0–76)	7.24 ± 13.80 (0–71)	0.79	0.375
Hatched eggs with dead larvae	4.06 ± 9.69 (0– 45)	2.04 ± 7.67 (0–42)	1.91	0.169

mortality in CPM (12.4%) compared to PPM (4.0%). The proportion of eggs containing dead larvae that have made an opening in the egg chorion during hatching averaged 3.0% for CPM and less than 1.0% for PPM, with no significant differences between the two species (one-way ANOVA, $F = 1.91$, $p = 0.169$).

Parasitoid species and parasitism rates in CPM and PPM eggs

Three species of egg parasitoids were identified in the eggs collected of the two *Thaumetopoea* species (CPM and PPM): two solitary species, *Baryscapus servadeii* (Domenichini) (Hymenoptera: Eulophidae) and *Ooencyrtus pityocampae* (Mercet) (Hymenoptera: Encyrtidae), and one polyembryonic species, *Trichogramma* sp. (Hymenoptera: Trichogrammatidae). The solitary species were found in the eggs of both CPM and PPM, while *Trichogramma* sp. was only found in PPM eggs.

The relative abundance of the parasitoids emerging from *T. bonjeani* and *T. pityocampa* eggs is presented in Table 3.

In CPM, parasitism was mostly carried out by *O. pityocampae,* which accounted for 98% of parasitoid emergence, while *B. servadeii* accounted only for 2%. In contrast, parasitism of PPM eggs was mainly driven by *B. servadeii*, accounting for about 48% of all the parasitoids, followed by *Trichogramma* sp. (38.7%), and *O. pityocampae* (13.1% of the parasitized eggs). At the egg batch level, the same observations were made, where the occurrence of parasitoids revealed significant differences between the two species (Figure 7).

Table 3. Mean (±SD) number of parasitoids and their relative abundance in *T. bonjeani* (CPM) and *T. pityocampa* (PPM) egg batches.

	CPM		PPM		F	P
Host	50		75			
Egg parasitoids	Mean ± SD (min–max)	Relative abundance (%)	Mean ± SD (min–max)	Relative abundance (%)		
Ooencyrtus pityocampae	9.54 ± 16.84 (0–73)	98.2	0.95 ± 3.40 (0–21)	13.1	18.47	0.000
Baryscapus servadeii	0.18 ± 0.83 (0–5)	1.9	3.49 ± 10.57 (0–66)	48.3	4.88	0.029
Trichogramma sp.	0	0	2.80 ± 8.54 (0–71)	38.7		

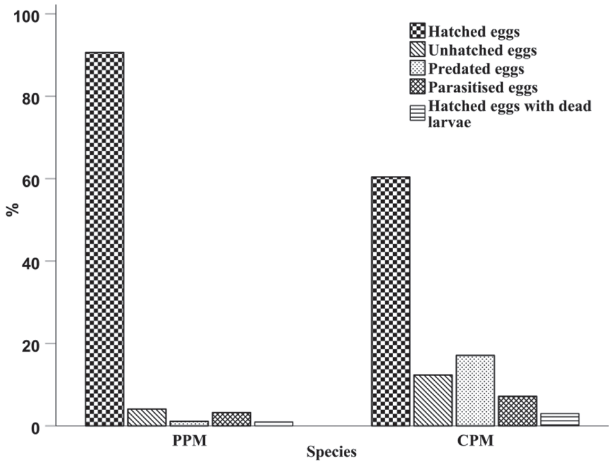

Figure 6. Hatching rates and mortality factors in *T. bonjeani* (CPM) and *T. pityocampa* (PPM) populations.

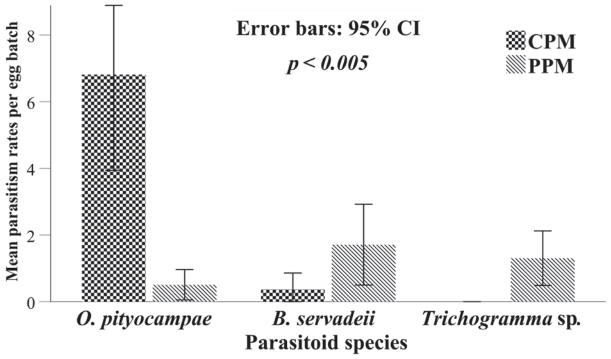

Figure 7. Mean parasitism rates of *O. pityocampa*, *B. servadeii* and *Trichogramma* sp. per egg batch in *T. bonjeani* (CPM) and *T. pityocampa* (PPM) populations.

DISCUSSION

Fecundity

Fecundity in processionary moths is defined as the number of eggs laid per batch (Battisti et al. 2015). Our results demonstrated a significant variation in fecundity between PPM and CPM, despite both species feeding on the same host, *C. atlantica*. PPM females exhibited significantly higher fecundity, with an average 223 eggs per batch. This value is consistent with the findings of El Mokhefi et al. (2021), who reported an average of 221 eggs per batch in the Chrea forest. In contrast, Ayache et al. (2021) found a lower average of 151 eggs in the same cedar stand, aligning with the cyclical population trends observed by Sbabdji et al. (2015). In comparison, CPM females laid an average of 136 eggs per batch. This value is lower than previously reported for the same species in the Djurdjura forest, where averages ranged from 157 to 173 eggs per batch (Rahim et al. 2016; El Mokhefi et al. 2021). In the populations of *T. bonjeani* developing in Moroccan cedar forests, El-Yousfi (1994) reported a higher average fecundity of 186 eggs. The fecundity of *T. bonjeani* is slightly higher than that of other summer processionary moth species, such as *T. ispartaensis*, which lays an average of 121 eggs per batch in Turkey (Avcı 2003; Küçükosmanoğlu 2019). However, the average fecundity of *T. pinivora* reported in Sweden was 164 eggs per batch (Tsankov et al. 1993). The egg diameters of the two species studied exhibited a significant variation. The *T. pityocampa* eggs are larger; with an average diameter of 1.1 mm. Similar values were reported by Sarikaya (2004) in Turkey. Schmidt et al. (1999) observed mean diameters varying between 0.99 and 1.13 mm in six localities in Spain and Portugal.

The fecundity of processionary moths can be influenced by both environmental and biological factors. Sebti et al. (2022) noted that temporal variations in fecundity are linked to the species' ability to adapt to environmental changes. Key environmental factors such as temperature and resource availability have been highlighted as critical determinants of fecundity (Masutti and Battisti 1990; Pimentel et al. 2012; Santos et al. 2013). Also, the quality of the host plant influences the fecundity, development and survival of herbivorous insects (Awmack and Leather 2002). In conifer species, the quality of needles varies over the seasons (Hatcher 1990). However, the same plant host was chosen for both species in order to minimize the effects of the host plant to the greatest extent possible, despite the inherent seasonal differences. The observed differences in fecundity between PPM and CPM in our study may be the result of the biological differences between the two species. Both species have asynchronous life cycles of different lengths. PPM larvae have a longer feeding period than CPM larvae, which favours bigger females' body size and consequently leading to an increased fecundity (El Mokhefi et al. 2021). According to the same authors, this could confer a competitive advantage to PPM in the case of potential cohabitation with CPM. Our results have shown that CPM presented smaller eggs than those of PPM. This observation seems to contradict the general trend described by Reavey (1992), which states that Lepidoptera species overwintering at egg stage are generally characterised by larger eggs, probably to ensure better survival in the harsh winter conditions. However, other factors may explain this difference. Reavey (1992) states that there is a strong positive correlation between adult body size and egg size with larger species generally producing larger eggs. In addition, the same author assumes that polyphagous species tend to lay larger eggs, potentially to favour a better capacity for adaptation which is the case of PPM that feed on both pine and cedar trees, whereas CPM is strictly monophagous, feeding only on cedar. These combined factors could explain the differences observed between these two species. In Lepidoptera, a trade-off is commonly observed between egg size and fecundity, with more fecund females generally producing smaller eggs (Smith and Fretwell 1974). However, PPM which is more fecund than CPM, lays larger eggs, which is contrary to this model. This could reflect an adaptation to winter development, where larger eggs would favour larval survival. Reavey (1992) notes that larger eggs produce larger larvae, which could improve their chances of survival. The trade-offs between the development period, the body size and fecundity of these two species, are the results of their adaptation to the environmental and climatic changes conditions. According to the life history of the genus *Thaumetopoea*, these biological and phenological distinctions and the difference in their spatial distribution seem to reflect the divergence of evolutionary strategies which enabled interspecific competition between the two species to be limited (Simonato et al. 2013; Kerdelhué et al. 2015; Basso et al. 2017).

Beyond fecundity, oviposition site selection also differed markedly between the species. PPM females showed a preference for thicker branches, averaging 4 mm in diameter, and typically laid eggs in 10 rows per batch, consistent with previous findings (Ayache et al. 2021). In contrast, CPM females selected thinner branches, averaging 3 mm in diameter, and deposited eggs in five rows. Similar preferences for thin branches have been reported in other summer species (Mirchev et al. 2017; Küçükosmanoğlu 2019).

These oviposition choices may reflect adaptive strategies aimed at optimizing larval survival, as branch characteristics can affect egg protection, microenvironmental conditions and the availability of feeding resources. In conifers, branch diameter is often positively linked to higher leaf area (Margolis et al. 1995), which may represent an advantage for young larvae in terms of the quantity of food available. According to Démolin (1969), PPM females select oviposition sites based on both the host species and the physical characteristics of the tree. According to Pérez-Contreras et al. (2008), PPM selects its host according to needle asymmetry, which is considered to be an indication of the nutritional quality and chemical composition of the leaves. Similarly, El-Yousfi (1989) reported that CPM females tend to oviposit at the tips of thin, hanging branches (approximately 2 mm in diameter), where the orientation of scales and homochromy with the substrate enhance protection against predation and winter falls. Ayache et al. (2021) further noted that the variability in PPM fecundity and oviposition site selection is influenced by environmental factors and haplotypic diversity between populations. This intraspecific variability suggests that genetic interspecific differences between PPM and CPM could also reflect divergent strategies of oviposition.

These behavioural differences align with the Preference-Performance Hypothesis (PPH), which posits that females of herbivorous insects select oviposition sites that maximize offspring performance and survival (Gripenberg et al. 2010). Female moths, guided by their physiological and adaptive capacities, choose egg-laying sites based on the availability and quality of resources, thereby enhancing the fitness of their progeny.

According to Mirchev et al. (2017), the total number of eggs, the length of the egg batch, and the number of rows in *T. solitaria* are interrelated. In our results, we also found a positive relationship between egg batch length and females fecundity in both species, with longer egg batches corresponding to a higher number of eggs. Similar observations have been reported for *T. pinivora* on *Pinus* species (Tsankov et al. 1993), *T. pityocampa* (Arnaldo and Torres 2006), and *T. wilkinsoni* (Nasr et al. 2013). Ayache et al. (2021) also observed a strong correlation between these two parameters on cedar trees in the Chréa forest. Furthermore, Mirchev et al. (2015) suggested that this correlation may also be influenced by the number of rows per egg batch. Supporting this, Tsankov et al. (1993) reported a positive association between the total number of eggs and the number of rows in *T. pinivora* egg batches.

Mortality Factors

Egg mortality varied between the two species and was primarily driven by three factors: unhatched eggs, predation, and parasitism. For CPM, the overall egg mortality was 39.6%, which is consistent with the findings of Rahim et al. (2016), who reported mortality rates of 47% in 2012 and 23.9% in 2013 within the same forest stand. The earlier study coincided with a period of severe infestation by *T. bonjeani*, during which an average of 21 egg batches per tree was recorded, with 27% of trees totally defoliated. In contrast, the current study recorded less than one egg batch per tree, indicating a significant decline in population density. In Moroccan cedar forests, the egg mortality rate reaches 20% (El Yousfi 1989). These values exceed those observed for the cedar processionary moth *T. ispartaensis* on *Cedrus Libani* in Turkey, where egg mortality rates ranged between 11% and 14% (Avcı 2003; Küçükosmanoğlu 2019).

In contrast to CPM, the PPM showed a lower egg mortality rate of 9.4% in the present study. However, mortality rates can vary with environmental conditions; for example, Messaadia et al. (2021) reported significantly higher PPM egg mortality rates of 33% and 25% at higher altitudes in the Chelia cedar forest (north-east Algeria).

The unhatched eggs rate includes egg abortion, sterile eggs, and parasitised eggs where parasitoids failed their development. This was the main mortality factor for PPM eggs, though low, with a rate of 4%. This rate was lower than the values reported by Sebti et al. (2022), who observed rates ranging from 5% to 45% between 2010 and 2014 in the same stand. For CPM eggs, unhatched eggs accounted for 12% of total mortality, which is significantly higher than the rates reported for *T. ispartaensis* eggs in Turkey, where rates were 2.9% and 3.7% (Avcı 2003).

Predation was higher in CPM eggs compared to PPM eggs. For PPM eggs, predation accounted for only 1.1% of total mortality, a value lower than the rates reported by Ayache et al. (2021), where predation reached 10% and 11% in the Chréa and Chelia cedar forests, respectively. In contrast, our results showed that predation was the primary mortality factor for CPM eggs, with a rate of 17%. Rahim et al. (2016) found that predation rates increased with rising CPM population density, contributing 5.2% and 7.4% to the overall mortality in 2012 and 2013, respectively.

The activity of parasitoids had a low impact on PPM eggs, with a recorded parasitism rate of 3.3%. Similarly, Bouzar-Essaidi et al. (2021) reported low average parasitism rates, accounting for less than 10% of the total egg mortality in both pine and cedar trees. In contrast, Messaadia et al. (2021) documented significantly higher parasitism rates, reaching 18% in the Chelia cedar forest. For CPM eggs, the parasitism rate was slightly higher, reaching 7.2%. Rahim et al. (2016) noted a more pronounced parasitism mortality during 2012 and 2013, with rates of 12% and 34.9%, respectively. Comparatively, Avcı (2003) recorded parasitism mortality rates of 11.3% on *T. ispartaensis* eggs.

The observed differences in egg mortality rates between PPM and CPM populations can be attributed to a complex interplay of ecological and evolutionary factors. One key explanation lies in the slow-growth–high-mortality hypothesis (Benrey and Denno 1997; Chen and Chen 2018), which posits that extended developmental periods in herbivorous insects increase exposure to natural enemies and environmental hazards, thereby elevating mortality risks. In the case of CPM, the embryonic stage spans the winter and extends into spring (Démolin 1988), rendering eggs particularly vulnerable to predation, parasitism, and harsh climatic conditions. This prolonged exposure is consistent with the elevated mortality rates observed, supporting the hypothesis.

In addition, the low population density of CPM recorded during the sampling period may have exacerbated predation. Scarce egg batches could have become focal points for predators due to limited alternative prey. While this relationship requires further clarification in CPM, similar patterns have been observed in PPM (Barbaro et al. (2013) reported increased predation by the Great Tit (*Parus major*) as PPM caterpillar densities declined. Conversely, Hódar et al. (2013) found that egg predation by generalist bush crickets was more influenced by egg location in predator-favourable microhabitats than by host density. This suggests that, in CPM, isolated egg batches placed in accessible locations could similarly face elevated predation pressure. Moreover, the structure and oviposition site of the egg batches influence highly their exposure to natural enemies. Ayache et al. (2021) demonstrated that flat PPM egg batches oviposited on branches with large diameters are more exposed and heavily parasitised than cylindrical egg batches laid on thinner branches. These differences may be a consequence of the adaptive females' choices to the climatic conditions of the forests. Additionally, the presence of egg scales may also limit parasitoid efficiency by serving as a physical barrier (Sebti et al. 2022).

Additional ecological and environmental factors may also play a role in the activity and diversity of parasitism and other natural enemies, including host density (Rahim et al. 2016; Sebti et al. 2022), altitudes (Ferracini et al. 2023), host fecundity, climatic conditions, and the phenology of both parasitoids and their hosts (Bouzar-Essaidi et al. 2021), host plant (Battisti 1989), and forest plant biodiversity (Mirchev et al. 2021). Although these parameters have not been discussed here, they are interesting avenues of research to explore.

In this study, three parasitoids species were identified from PPM eggs: *O. pityocampae*, *B. servadeii* and *Trichogramma* sp. These same species were previously reported in Algeria from PPM eggs on cedar host by Zamoum et al. (2017); Ayache et al. (2021), Messaadia et al. (2021) and Sebti et al. (2022). In contrast, Bouzar-Essaidi et al. (2021) recorded only the generalist *O. pityocampae* and the specialist *B. servadeii* across 27 pine and cedar forests sites, with *B. servadeii* being the dominant species. Similarly, our results revealed that parasitism activity was primarily driven by *B. servadeii* (48.8%), followed by *Trichogramma* sp. (38.7%), while *O. pityocampae* accounted for only 13.1% of egg parasitism.

For CPM egg batches, the same parasitoid species, except *Trichogramma* sp., were recorded. Notably, *Trichogramma* sp. was previously identified as a CPM egg parasitoid in the same cedar forest, along with the hyperparasitoid *Chartocerus* sp. (Rahim et al. 2016). Among the recorded species, *O. pityocampae* was identified as the dominant cause of egg parasitism, with an incidence rate of 98.2%. These results are consistent with the observations reported by Rahim et al. (2016) in Djurdjura forest, as well as those of Avcı (2003) for *T. ispartaensis* in Turkey.

The variability observed between the occurrence and dominance of *B. servadeii* and *O. pityocampae* in CPM and PPM egg batches may result of their adaptive behaviour in response to environmental conditions. According to Hezil and Chakali (2025), the host selectivity of these two parasitoids species depends on their intrinsic behavioural traits, environmental conditions and egg scales characteristics. Their degree of variation in temperature tolerance, which is higher in *B. servadeii*, could partially explain the dominance of *O. pityocampae* in CPM egg batches, which are laid later in the season. In addition, *B. servadeii* is considered to be a parasitoid relatively specific to PPM, exhibiting a strong ecological and behavioural affinity with its host, which could explain its higher rates of parasitism on this species compared with CPM (Simonato et al. 2019; Sebti et al. 2022).

The co-occurrence of *T. bonjeani* and *T. pityocampa*, which share the same ecological niche, exposes their eggs to the same natural enemies (Zamoum et al. 2017). However, the asynchrony of their life cycles provides temporally availability of resources for generalist parasitoids, thereby favouring their persistence and effectiveness and contributing to the regulation of the two populations and mitigating the risk of outbreaks (Figure 8).

In conclusion, this study provides a comparative analysis of reproductive strategies and egg mortality factors between the pine processionary moth (PPM) and the cedar processionary moth (CPM) on *C. atlantica.* Significant differences were observed in fecundity and egg mortality between the two species. The PPM exhibited higher fecundity, characterized by larger egg batches and a preference for oviposition on thicker branches. In contrast, the CPM displayed lower fecundity and tended to oviposit on thinner branches.

Egg mortality factors also differed notably between the two species. The CPM experienced higher overall mortality, primarily due to predation and parasitism, with predation being the leading cause. In PPM, the main cause of egg mortality was unhatched eggs, while parasitism rates remained relatively low. Conversely, the CPM showed higher parasitism, with *Ooencyrtus pityocampae* identified as the dominant parasitoid. These findings contribute valuable insights into the reproductive strategies and ecological interactions of these processionary moths and may inform future management strategies and ecological research. However,

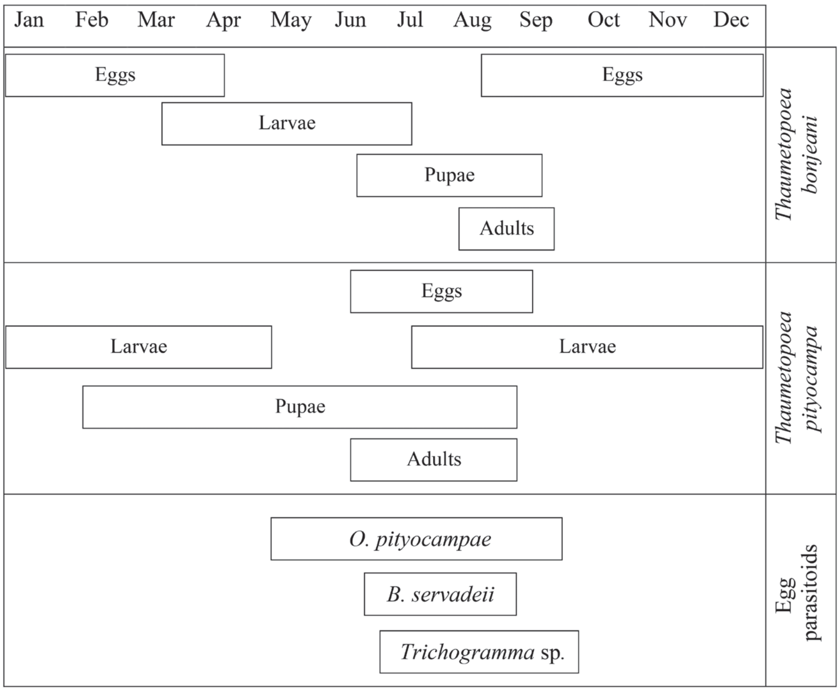

Figure 8. Life cycles of *T. bonjeani* and *T. pityocampa* in Atlas cedar stands in Algeria and activity periods of their main egg parasitoids (*O. pityocampae*, *B. servadeii*, and *Trichogramma* sp.).

given the annual variability in population dynamics and ecological interactions, further long-term studies are needed to confirm and clarify these hypotheses.

ACKNOWLEDGMENT

The authors sincerely thank the Faculty of Natural and Life Sciences and Earth Sciences at the University of Bouira, as well as the Department of Agricultural and Forest Zoology at the Higher National School of Agronomy of Algiers for providing access to their laboratories and equipment. We are also grateful to Y. Mahri and S. Ayache for their valuable assistance in the field and to S. Kassouar for her insightful suggestions and support during the manuscript writing process. Finally, we extend our appreciation to the two anonymous reviewers for their constructive comments, which significantly improved the quality of the manuscript.

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