Zoodiversity, **55**(3): 239–250, 2021
DOI 10.15407/zoo2021.03.239

UDC 595.78:582.475.2(65)

EGG BATCHES PARASITISM OF PROCESSIONARY MOTH, *THAUMETOPOEA PITYOCAMPA* (LEPIDOPTERA, THAUMETOPOEIDAE), FROM TWO ATLAS CEDAR ECOTYPES IN ALGERIA

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Egg Batches Parasitism of Processionary Moth, *Thaumetopoea pityocampa* (Lepidoptera, Thaumetopoeidae), from Two Atlas Cedar Ecotypes in Algeria. Ayache, S., El Mokhefi, M., Bonifácio, L., Chakali, G. — In the Atlas cedar forests located on the northern massifs of the Blidean Atlas and at the eastern extension of the Saharan Atlas, 79 egg batches of processionary moth *Thaumetopoea pityocampa* (Denis & Schiffermuller, 1775) were collected during the summer period from two sites: Chréa National park (46), and Ouled Yagoub forest (33). To assess the effect of the egg batches characteristics on the parasitism, the eggs were monitored after the hatching of the larvae and/or the emergence of the parasitoids. The average number of eggs/batches in the Ouled Yagoub site (184 eggs) was significantly higher than of the population of Chréa (151). Data analysis showed that the means comparisons of the hatched and unhatched number of eggs between the two sites were significant. In the case of the population of Chréa, the egg mass was laid in the form of a cylinder on twigs of relatively small diameters while for the population of Ouled Yagoub eggs were laid in the form of plates on twigs of larger diameter, thus more exposed to parasitoids. For the two populations, three active egg parasitoids were identified: *Ooencyrtus pityocampae* (Mercet, 1921) (Encyrtidae), *Baryscapus servadeii* (Domenichini, 1965) (Eulophidae), and *Trichogramma embryophagum* (Hartig, 1838) (Trichogrammatidae), the most dominant. These parasitoids were heterogeneously distributed on the egg batches collected in the cedar's plantation of the Chréa, but homogeneously on the egg batches collected in the Ouled Yagoub cedar forest. The activity and distribution of parasitoids on the egg-laying surface are influenced by the form on the branch chosen by the female.

Key words: processionary moth, fecundity, egg parasitoids, *Cedrus atlantica*.

Introduction

The winter pine processionary moth, *Thaumetopoea pityocampa* (Denis & Schiffermuller, 1775) is the major defoliator of pines around the Mediterranean basin (Demolin, 1969). During gradations, this pest is capable of attacking vigorous trees and deteriorates their health (Huchon & Demolin, 1971). Currently, populations of this insect attack mainly, Aleppo pine (*Pinus halepensis* Mill.) in the semi-arid area and Atlas cedar (*Cedrus atlantica* Manetti) in sub-humid elevation area stands causing considerable economic losses (Sbabdji et al., 2009). Many authors report that increasing infestation rates and the environmental damage caused by processionary moth within its recent distribution range is related to climatic changes (Battisti et al., 2005; Battisti et al., 2006; Toffolo et al., 2006; Rousselet et al., 2010). By genetic structure processionary moth is presented by two well-geographically localized clades: the *pityocampa* clade, identified in Europe, Morocco, and south-western Algeria; and the ENA (Eastern North Africa) clade, found in the north-eastern part of Algeria, northern Tunisia, and northern Libya, in the humid, sub-humid, and semi-arid climates (Kerdelhué et al., 2009; El Mokhefi et al., 2016). In Algeria, the expansion of processionary moth was favored by the Aleppo pine (*Pinus halepensis*) plantations along the Saharan Atlas as part of 'Barrage vert', started in 1983 (Zamoum et al., 2015).

With global warming, the processionary moth, which has become a study model, is developing a wider horizontal and vertical expansion across the Mediterranean area (Battisti et al., 2005).

In its natural biotope, *T. pityocampa* is a monovoltine species, but can extend its development over two or more years, depending on the altitude, according to the intensity of the diapause and the environmental conditions (i. e. temperature and insolation) (Geri, 1983).

In recent years, populations of this insect have been developing continuously and the consequences of defoliations have become worrying even on cedar stands, as noticed in the Chréa National Park (Sebti & Chakali, 2014).

Reproduction takes place in summer, and the larvae develop in autumn and winter. The life cycle is carried out in two phases, the aerial (oviposition and larval development through five stages) and the underground phase (pupation) (Huchon & Demolin, 1971).

Female's choice of egg-laying site depends on some parameters such as low-density stands and high trees at the edge of the stand (Demolin, 1969; Régolini et al., 2014). In addition, the quantity and quality of nutritional resources determine the selection of the host that offers a better chance for good larval development, and therefore an enhanced female fertility (Devkota & Schmidt, 1990; Thompson & Pellmyr, 1991; Tiberi et al., 1999). Also, the physical and chemical characteristics of the host plant can influence the selection of the egg-laying site (Renwick & Chew, 1994). This choice is crucial as it affects the insect's population dynamics and that of its egg parasitoids, which regulate its populations' level (Morel, 2008).

Egg parasitism can be noticed on 50 % of eggs during gradations (Battisti et al., 2015). *Ooencyrtus pityocampae* (Hymenoptera, Encyrtidae) and *Baryscapus servadeii* (Hymenoptera, Eulophidae) are known as the most active parasitoids in the Mediterranean region (Avci, 2003; Mirchev et al., 2007; Bouchou & Chakali, 2014; Hezil et al., 2018).

Despite various studies on the biology and ecology of this defoliator, sparely information is available on the morpho-biometry of eggs, its relation with the host, and how affects parasitoids' activity. The main objective of the study was to assess the characteristics relating to the structure of egg batches in two natural Atlas cedar stands of Chréa and Ouled Yacoub; considering (i) twig diameter, (ii) egg batch length, (iii) number of eggs per batch, and (iv) number of parasitized eggs per batch. In addition, information on the relationship between the egg batch form and the specific distribution of embryonic parasitoids was discussed. From the results obtained, the relationship was found between the various environmental parameters and the choice of egg-laying sites in the analyzed ecotypes.

Material and methods

Study sites

The sampling was carried out in 2017 in two natural Atlas cedar stands (table 1).

Chréa plot is a part of the National Park that covers an area of 7.000 ha, located on the Tellian Atlas, 50 km south-west of the capital Algiers. The locality is under a subhumid bioclimate, with average temperatures of 5 °C in winter and 22 °C in summer, and an average annual rainfall of 700 mm. The locality of the Ouled Yagoub plot belongs to Chelia National Park that extends over an area of 3.000 ha on the eastern part of the Saharan Atlas, at 500 km south-east of the capital. This area is located in a subhumid bioclimate, characterized by average annual temperatures of 7 °C and 25 °C in winter and summer, respectively and an average annual rainfall of 550 mm.

Collection and preparation of biological material

A total of 79 eggs batches were collected during the summer period (46 for the Chréa site and 33 for Ouled Yagoub). Egg batches have a cylindrical form of few centimeters in length, laid on twigs of various diameters (fig. 1, A; B). Along a linear transect, one twig containing a batch of eggs was sampled using a lopper and individually stored in glass tubes (10 cm long and 1 cm diameter), numbered, and capped with fine cotton to allow air circulation. Egg batches found in thicker twigs, exceeding the tube diameter, were stored individually in transparent cups (8 cm long and 5 cm diameter) and closed with a fine mesh fabric. The material thus

Table 1. Sampling sites location

Sites	Geographical coordinates			
	Cardinal position	Latitude	Longitude	Elevation (m)
Chréa	(NW)	36°26´02.0˝ N	2°53´00.0˝ E	1438
Ouled Yagoub	(SE)	35°19´21.0˝ N	6°37´53.0˝ E	2096

prepared was stored in laboratory conditions at 25 ± 2 °C temperature, and 70 ± 5 % of relative humidity. Eggs were monitored daily for hatching larvae and parasitoids emergence, over a period of 60 days.

The meconium was used for primarily identification of the parasitoid species according to the method proposed by Tsankov et al. (1996). The shape of meconium varies depending on the species. For *O. pityocampa*, it is a flat yellow disc while that of *B. servadeii* is a single ball stuck on the chorion of the egg.

Adult wasps were identified by G. Chakali and verified by B. Pintureau (UMR INRA/INSA de Lyon — Biologie Fonctionnelle) and by molecular analysis carried out by the team of Dr. Ris in Nice (Antibes).

Measurements and egg counting

The diameter of the supporting twig and the egg batch length were measured using an electronic caliper.

Protective scales were carefully removed from egg batches using adhesive tape to count the total number of eggs per batch, under a binocular magnifier. Mean values were used to assess female fertility in the two localities.

The egg batches were divided into three parts using a marker: upper, middle, and basal, in order to determine the parasitoids distribution pattern. The upper part of the egg mass considered is the location towards the top of the branch.

Three types of eggs were determined for each batch (fig. 1, C): 1) Non-parasitized eggs, recognizable by the rounded shape and the whitish color. After completing their embryonic development, larvae hatch leaving a circular hole. 2) Empty eggs have a pure yellowish color. Their sterility is usually due to embryonic fall (mortality), or because the egg contains a diapausing parasite. 3) Parasitized eggs, which become blackish a

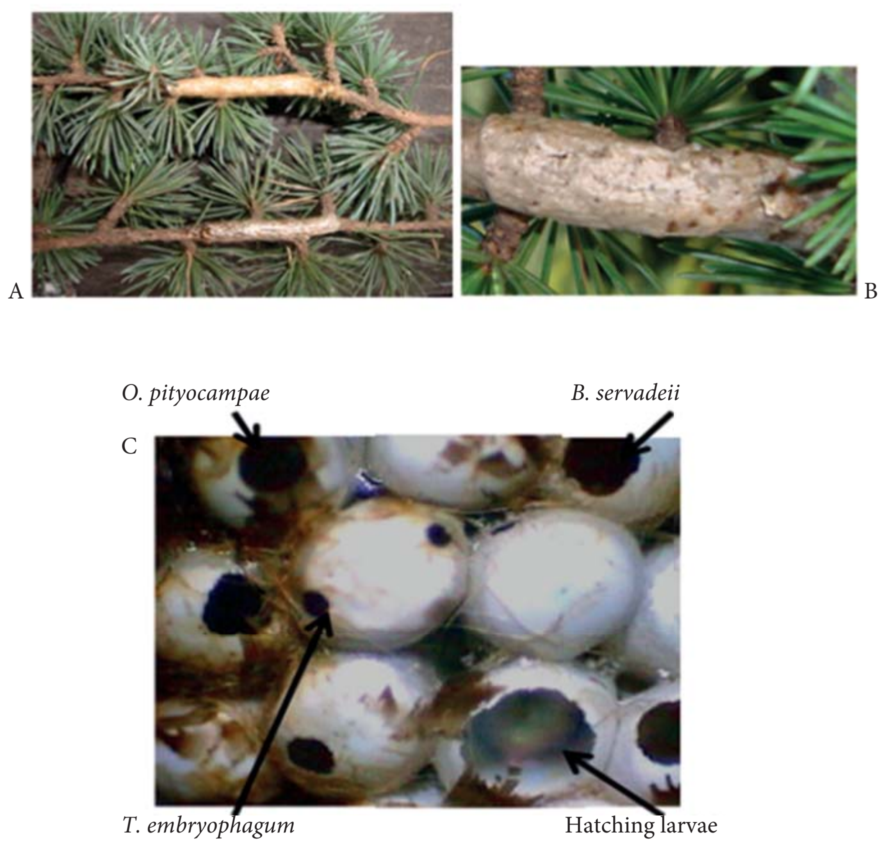


Fig. 1. Eggs batches of *Thaumetopoea pityocampa*: A — cylindrical form; B — egg batches in thick twigs; C — types of eggs.

few days after being parasitized. The holes left by the parasitoid after emergence is relatively smaller than those produced by larval hatching. Inside of the parasitized egg remains of the host insect embryo and meconium left by the parasitoid just before emergence can be found.

The emergence of *T. embryophagum* is characterized by very small round exit holes (one to three per egg), compared to other parasitoids (Tsankov et al., 1996).

Data analysis

The characterization of the egg-laying of *T. pityocampa* involves two variables groups: variables related to the moth's fertility, and host tree variables, i. e. diameter of twigs carrying the egg batch. Linear regressions were performed to calculate the correlations and the equations which significantly describe the relationships between the number of eggs and the size of the egg batches. A descriptive analysis and unidirectional analysis of variances (ANOVA), with results interpreted at the 5 % error, were carried out to assess the effect on the moth's populations of the variables selected for the two surveyed sites. All analyzes were carried out using XLSTAT (Version 2016.02.28451) and STATISTICA software (Statsoft Inc. 2003; version 6.0).

Results and discussion

Analysis of the biological material

The data collected from the two study sites on the biometrics of the support branches, batch characteristics and the count of the egg's categories are presented in table 2. All variables considered presented statistical significant differences between sites. The average diameters of the twigs chosen by the females for laying eggs were significantly bigger in the cedar forest of Ouled Yagoub than in Chréa, with 6.5 mm and 4.1 mm respectively. The number of rows laid in parallel by the females was also bigger in Ouled Yagoub but with higher variability (4 to 24 rows) when compared to Chréa (5 to 11 rows).

A remarkable adaptation was noted on the females of the Ouled Yagoub site which have the ability to cling to thick twigs to lay the eggs and easily maintain themselves on thicker branches than those from the Chréa area. This variability observed between the studied populations is associated of environmental factors, and the ecotype of each population.

Quantitatively, the female fertility estimated from the total number of eggs per batch was significantly higher in the Ouled Yagoub site (184) compared to the Chréa population (151). Considerably greater average hatching of 94 eggs/batch was obtained from the biological material collected in Chréa, despite greater fertility of the population

Table 2. Descriptive statistics related to twigs, batches, and eggs categories, and the corresponding statistical significance between sites

Sites	Chréa		Ouled Yagoub	
Sample sizes	46		33	
Descriptives	mean ± SD	(min–max)	mean ± SD	(min–max)
Twig diameter, mm***	4.1 ± 1.1	2.2–6.6	6.5 ± 3.4	2.5–13.7
Batch length, mm*	23.8 ± 4.8	12.9–34.1	27.7 ± 7.6	20–59.1
Total eggs***	151 ± 26	84–235	184 ± 55	103–335
Rows/batch***	7 ± 2	5–11	11 ± 5	4–24
Hatched eggs*	94 ± 52	0–206	62 ± 61	0–216
Non hatched eggs***	47 ± 39	0–157	111 ± 75	5–310
Parasitized eggs*	10 ± 14	0–70	11 ± 10	0–39

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

of Ouled Yagoub, where the mean number of unhatched eggs was more than twice the number of unhatched eggs in Chréa, with 111 and 47 respectively. This could be explained by the collection of egg-batches at altitude, which often results in non-fertile eggs as reported by Démolin (1969). Likewise, the very often severe conditions at altitude, where minimum temperatures can reach −10 °C, could have a negative influence on embryos. In the case of the Chréa population, the laying was in the form of a cylinder while for the Ouled Yagoub population, the egg batches were rather flat, therefore more exposed to the parasitoids, with significant impact.

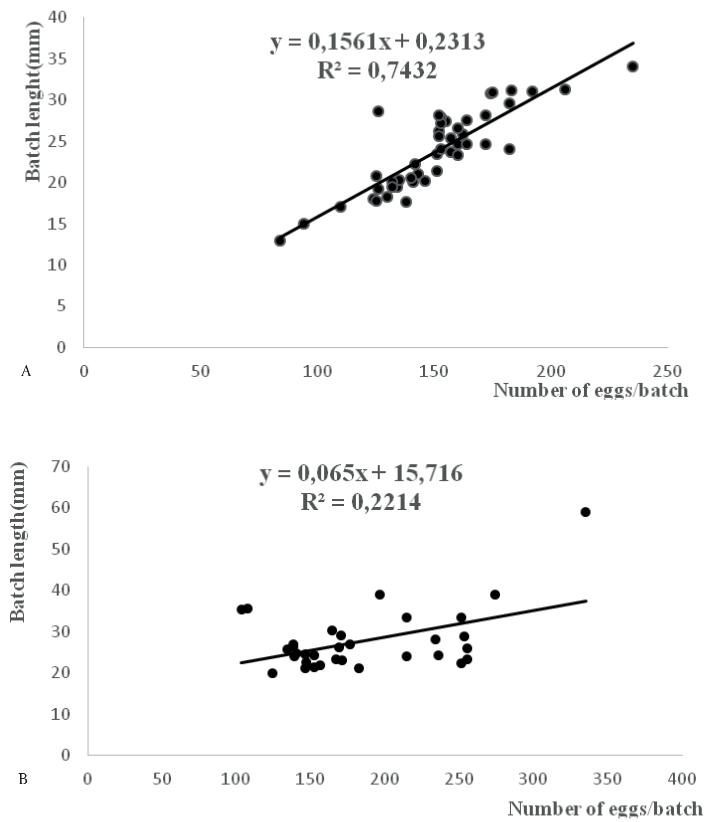


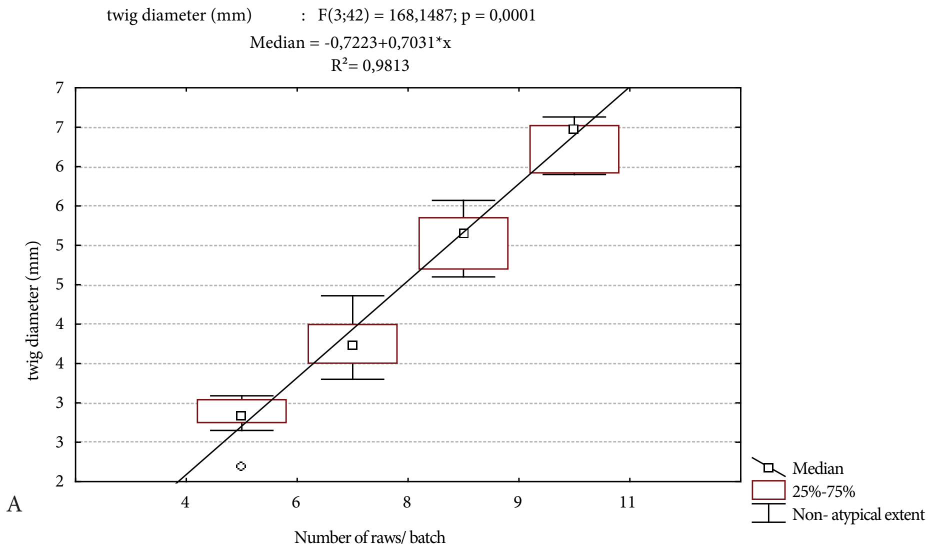
Fig. 2. Relationship between batch length and the number of eggs in Chréa (A) and Ouled Yagoub (B).

Correlation between batch length and the total number of eggs

A high positive correlation between the batch length and the number of eggs was evaluated for the population at Chréa ($R^2 = 0.7432$), while for the population of Ouled Yagoub, the correlation was also positive yet relatively less significant ($R^2 = 0.2214$) (fig. 2). Despite the higher fertility of the population of Ouled Yagoub, the arrangement of the eggs on the twigs is not as appropriate as is Chréa population.

Table 3. Importance of the embryonic parasitoids of *Thaumetopoea pityocampa* obtained in the egg batches collected in the study sites

Sites Parasitoïds	Chréa Sample sizes (46)		Ouled Yagoub Sample sizes (33)	
	mean ± SD (min–max)	relative abondance, %	mean ±SD (min–max)	relative abondance, %
Ooencyrtus pityocampae	2 ± 2 (1–18)	11	6 ± 4 (2–21)	17
Baryscapus servadeii	5 ± 5 (2–58)	28	3 ± 3 (2–22)	29
Trichogramma embryophagum	50 ± 43 (9–129)	61	14 ± 15 (11–64)	54



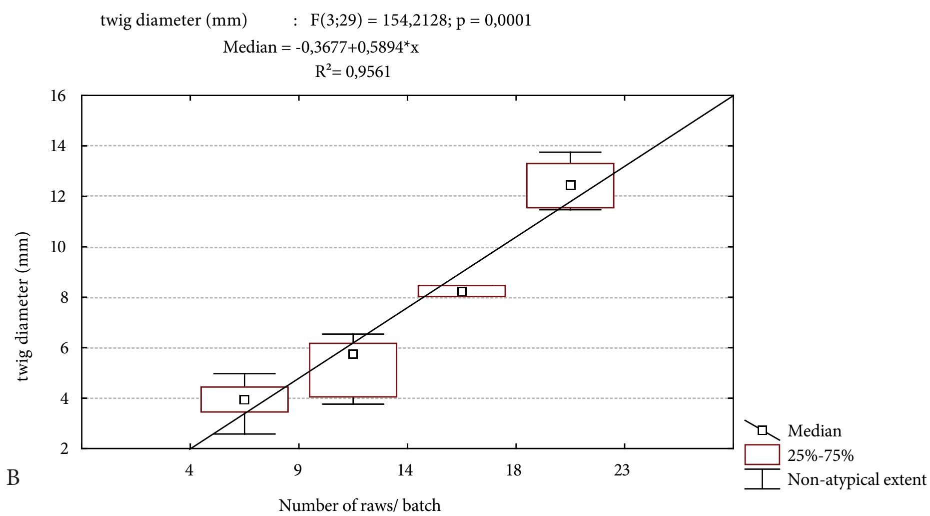


Fig. 3. Distribution of the number of egg rows in relation to the twig diameter in Chréa (A), and Ouled Yagoub (B).

Correlation between the twig diameter and the number of rows of eggs/ batch

The relationship between the size of the branches chosen by the females and the number of ordered rows laid is illustrated in figure 3, and for both sites, the number of egg rows is highly correlated to the median values of the supporting branches, revealing the female's strategy in the laying and arrangement of eggs in relation to the host characteristics.

Emergence and activity of parasitoids

In the both studied sites, three species of embryonic parasitoids were identified from the biological material analyzed. These are two solitary Chalcidoidea: *Baryscapus servadeii* (Domenichini) (Hymenoptera, Eulophidae) and *Ooencyrtus pityocampae* (Mercet) (Hymenoptera, Encyrtidae). The third species noted is *Trichogramma embryophagum* (Hartig) (Hymenoptera,Trichogrammatidae).

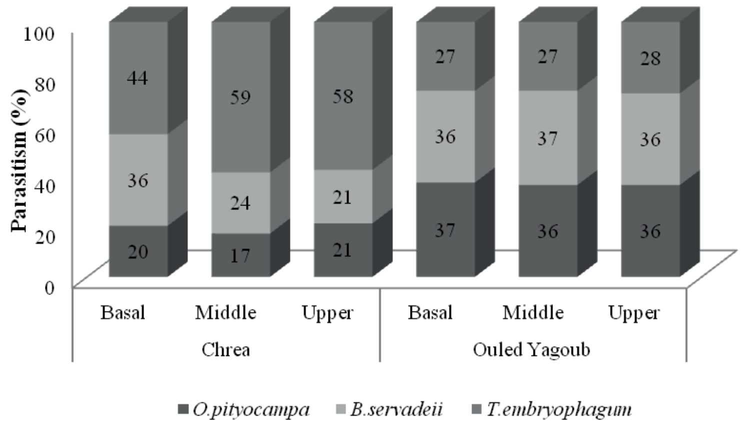


Fig. 4. Distribution of parasitoids on the egg-batch surface.

For both processionary moth populations studied, *T. embryophagum* remains the predominate parasitoid, not only several adults emerged from the same exit hole but also some eggs showed two exit holes (table 3).

Regarding the seasonality of the parasitoid species, the individuals of *B. servadeii* had an early emergence than the species *O. pityocampa* and *T. embryophagum.*

Distribution of parasitoids on the egg-batch surface

The three listed parasitoids distributed heterogeneously on the egg batches collected in the Chréa cedar plantation, while a more homogeneous parasitoids distribution was observed on the eggs from Ouled Yagoub cedars. The activity of parasitoids on the batch surface is influenced by its form since egg batches on thicker branches usually have a flat shape, more exposed and easier for the parasitoids action (fig. 4).

Hierarchical classification of the variables considered

The aggregation distance as a function of consecutive steps shows the similarity of neighboring variables, number of rows/batches, diameter of twigs (fig. 5). The number of parasitized and hatched eggs is closely related to the morphological characteristics of eggs. The more the batch is flat. The variability of the parameters considered is closely related to the sites prospected.

The egg-laying behavior of the processionary moth females is dependent on several environmental variables and reveals higher fertility in the cedar forest. The winter processionary moth females have the ability to detect favorable biotopes for the release of their eggs where their progeny would have enough food for their development. It is recognized that females of *T. pityocampa* during their cycle lay their eggs in a single sequence. The number of eggs per batch corresponds to the fertility of a female as described by Mirchev and Tsankov (2005), Battisti and al. (2015). Data analysis collected on the fertility of females on the Atlas cedar confirmed the correlation mentioned by Özkazans (1987) who noted that the fertility of females increases with altitude. The studies carried out by Parker and Begon (1986), Freese and Zwolfer (1996), Tiberi et al. (1999) showed that the quality and quantity of resources available in the host plant are determinant ecological factors that influence the eggs productivity of *T. pityocampa*. Demolin (1969) noted that the fluctuation of the population is related to various factors, particularly climate, altitude, food, and the antagonists. This result shows that the site choice is a part of a strategy evolutionary adopted by the female for the protection of its progeny. Whatever the diameter of the branch, fertility is more substantial at altitude. Tilman (1980) noted that the female chooses the site for laying eggs that can maximize the survival of its offspring due to enough amount of resources available.

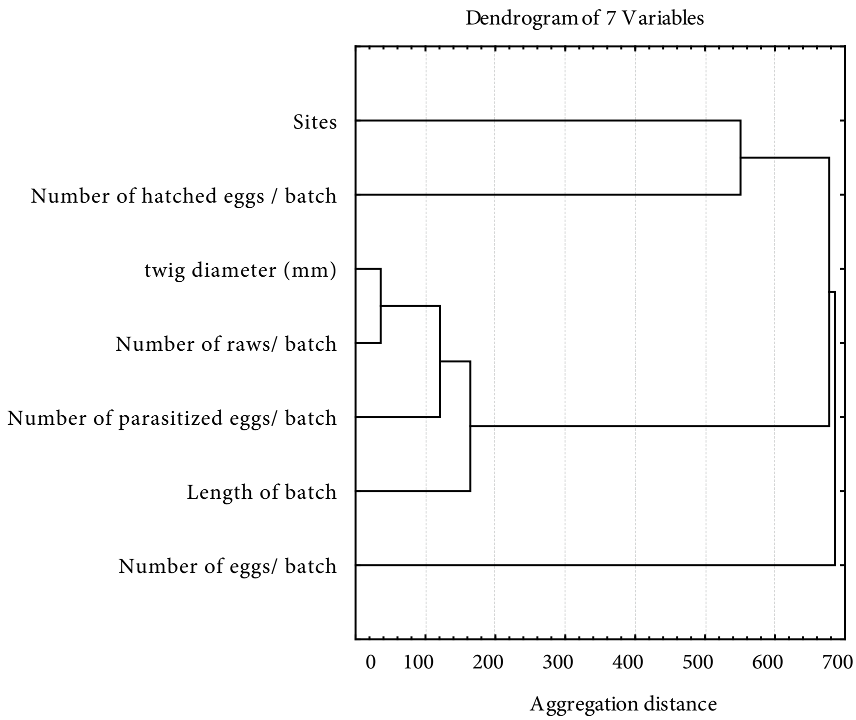


Fig. 5. Hierarchical classification of the variables considered.

The variability in the choice of the twig diameters can be explained by the haplotypes' diversity of the species in its biotope. Both populations considered are of ENA clade (Kerdelhué et al., 2015). According to the mitochondrial haplotypic network of ENA clade, the Chréa population contained essentially one haplotype (E3), thus than a limited set of 3 haplotypes (E1- E4- E8). In contrast, the population of Ouled Yagoub had one major haplotype (E1), and two haplotypes with low frequencies (E9- E8) (El-Mokhfi et al., 2016). The females which evolve in the cedar forest of Ouled Yagoub, have the particularity to seek more the lower part of the relatively thicker branches to carry out their flat-shaped egg-laying, in order to protect their offspring from severe winter conditions, particularly during snowfall, which often lasts two months.

This investigation reports the importance of fertility and the choice of twigs by females to lay their eggs along an altitudinal gradient in two natural ecotypes of the Atlas cedar, *Cedrus atlantica*. Likewise, in the strategy of parasitoids, the shape of the egg-batch on the twig has a decisive role in the successful establishment, this particularity may have a direct regulating effect on the proliferation of processionary moth populations (Biliotti, 1958; Battisti, 1989; Tsankov et al., 1999; Mirchev et al., 2012; Mirchev et al., 2015).

Halperin (1990) mentioned that the survival of polyphagous parasitoids such as *O. pityocampae* does not require synchronization between their emergence and the availability of unhatched eggs of the processionary caterpillar. In contrast, a relay synchronization is necessary for *B. servadeii* because this parasitoid is endowed with specificity towards the species of processionary moths in their range of distribution.

For the Ouled Yagoub population, the two generalist parasitoids *O. pityocampae* and *B. servadeii* showed comparable frequencies. This suggests that the activity to be detected and the ease of parasitism of eggs by these polyphagous parasitoids is related to the availability of flat-form egg-batches on the twigs. Mirchev et al. (2015) showed that the action of polyphagous parasitoids encompasses a wide host range and their presence in a specific biotope is accidental. A different antagonism between the parasitoids was observed concerning their capacities to parasitize the eggs of the processionary moth in the prospected sites. Interspecific competition is determined by various ecological factors related to the entomological diversity which ensures the availability of alternative hosts. Mirchev and Tsankov (2005) noted that *B. servadeii* searches for processionary eggs at the laying time, whereas for *O. pityocampa* this period is speedy. In this regard, Halperin (1990) confirmed the idea that the phenology of *O. pityocampae*, unlike that of *B. servadeii*, is not synchronized with of *T. pityocampa.* A comparable specific diversity of embryonic parasitoids has been noted in various species of the genus *Thaumetopoea* such as *T. bonjeani* in Algeria (Rahim et al., 2016), and *T. pinivora* in Spain (Battisti et al., 2015). An absence of *B. servadeii* in *T. ispartaensis* eggs has been noted in Turkey (Avcı, 2003). Other species of parasitoids belonging to the superfamily Chalcidoidea were recorded in low numbers on *T. pityocampa* eggs by various authors. Mirchev and Tsankov (2005) in the pine forests of Greece, Tiberi et al. (2015) in the pine forests of Tuscany in Italy identified the species of *Baryscapus transversalis*, *Anastatus bifasciatus*, and *Pediobius bruchicida*. Also, the species *Ooencyrtus telenomicida* was noted on egg-batches collected in the pine forests in southern Italy (Tiberi, 1990). In the cedar plantations surveyed, the period of emergence of *O. pityocampa* and *B. servadeii* was synchronized with the period of oviposition of *T. pityocampa* in July–August. This is comparable with the study conducted by Zamoum et al. (2015) in the Aleppo pine forests of the sub-Saharan region in Algeria. Arnaldo and Torres (2006) in the pine forests of northern Portugal reported that the two above-mentioned parasitoids emerge in two periods, the first in the fall of the same year during the egg-laying period, and the second in the spring of the year following a winter diapause. This explains the number of eggs quantified with diapausing parasitoids in the biological material analyzed.

The distribution of parasitized eggs is an indicator of their acclimatization to this host. The various parts of the egg-batches are searched indiscriminately by *B. servadeii* from the Chréa site, which expresses the adaptability of the species. Masutti (1964) noted that this parasitoid had the ability to slip between the protective scales to reach the eggs. Likewise, Biliotti (1958) considered that the presence of scales is a protective barrier for encyrtids, whereas they do not present an obstacle for eulophids. It is common for the eggs at both ends of the batch to be partially covered by scales and this can facilitate the action of the parasitoids *O. pityocampa* and *T. embryophagum.* In this regard, it should be noted that there are reports related to the distribution of eggs parasitized by the various antagonist species. Kitt and Schmidt (1993) found that *O. pityocampa* mainly seeks the apical part of the egg-batch, while *B. servadeii* prefers the basal part, but the results obtained by Mirchev et al. (2012) showed that the upper parts were the most sought after by parasitoids. A homogeneity in the distribution of embryonic parasitoids was noted in the biological material from the Ouled Yagoub area.

The shape of the egg-batch and the architecture of the protective scales has an essential role in the distribution of parasitoids. These results are reported by Arnaldo and Torres (2006) who noted that the egg-batch structure of the pine processionary moth and the associated parasitoid species are influenced by the morphology of the spawning supports of the various potential hosts of the pine processionary moth. This is valid for the cedar twigs, particularly for the Ouled Yagoub site. Morphobiometric data on the protective scales could further confirm the choice and distribution of parasitoids on the egg-batch surface.

The variability of fecundity and the effect of the twig's diameter on the selection by the laying females between the populations of the processionary *T. pityocampa* in the prospected areas are under the aegis of several factors including environmental factors, and probably on the haplotypic diversity of the species within its biotope. Females have different physiological and adaptive capacities for the development of their respective eggs and choose sites that can maximize the larval survival of their offspring through the amount and the quality of available resources.

Abbreviations

ENA clade: Eastern North Africa clade; NW: North West; SE: South East.

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Received 18 November 2020
Accepted 5 May 2021