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Fecundity of the pine processionary moth *Thaumetopoea pityocampa* (Lepidoptera: Notodontidae) at the southern edge of its distribution range

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Abstract: Analysis of annual and plot variations of egg batches number of *Thaumetopoea pityocampa* at the southern limit of its distribution area and in *Pinus halepensis* afforestations situated in the Algerian sub-Saharan region showed that its fecundity depends on the density of its population, plots, years and interaction of plots-years. It appears that the high average abundance of egg batches/trees during the outbreak period of this pest insect exceeds 24. The real fecundity is the lowest in the Mediterranean Basin and suggests that local adaptation can occur. The low fecundity is not an obstacle to caterpillar survival under different selection pressures. It is compensated by merging of colonies during the larval cycle. Moreover, in this study we noted a significant correlation between the number of eggs and the size of egg batches deposited on needles or around small pine branches. Size of egg batches is also intimately linked to the length of adult female forewings, fresh weight of females and weight of their pupae. Females with a biennial cycle have a low potential fecundity compared to those with an annual one.

Key words: fecundity; egg batches; *Thaumetopoea pityocampa;* afforestation; semi-arid; *Pinus halepensis*

Introduction

Pine processionary moth (PPM) (*Thaumetopoea pityocampa* Denis & Schiffermüller, 1775) is a defoliator lepidopteran causing economic losses to pine and cedar forests in the Mediterranean Basin and other Southern European areas. The adults emerge in summer and females emit a sex pheromone, so mating is immediately followed by oviposition. Embryonic development lasts for 30–45 days, and the gregarious larvae develop during winter and build a tight and silky nest on the periphery of the tree to get a good insolation. At the end of winter, the mature larvae descend to pupate in the soil for diapause until July–August. However, in certain areas, they descend in early January. Some pupae have a prolonged diapause lasting 1–6 years.

The eggs are laid during summer around two or more pine needles or small twigs and normally, only one cluster per female, rarely two. They are deposited in a one layered cylindrical cluster containing more than 100 white, round and ovoid eggs. The laying kinetics of eggs can be detected: they are deposited from the base of needles to the top. At the laying time, the female wraps her eggs with the colleterial gland excretions, and eggs are glued together with support and protective scales. Egg clusters come off very easily from the support, but eggs are very difficult to separate. Because of size and color of scales, egg masses become inconspicuous with buds or branches of the host trees. Scales which are attached from their bases to the eggs reduce the pressure from predators and protect eggs from the sun and rain (Milani 1990). Moreover, color and size of scales differ according to origin of female PPM. In general, they are round and large in the sub-Saharian afforested area. However, they are of honey colour in natural pine forests, and small, more elongated and honeyed in cedar forests. As egg batches stay more than one year on the host trees after caterpillars hatch, their study is easy.

Phylogenetically, the populations of the PPM which are studied belong to the third clade identified by Kerdelhué et al. (2009). It consists of 24 European haplotypes, from Spain and Portugal to Greece (with a notable exception of Crete), together with the 7 haplotypes found in Morocco and South Algeria. This ecological study is aimed to investigate typical characteristics of egg batches of the PPM which are not well known from the pine forests located in the southern limit of its distribution range (i); dispersion of oviposition sites of the egg batches in *Pinus halepensis* Miller plantations (ii); and variations in potential fecundity of females and simplified estimation of egg numbers (iii). It could give a better understanding of the tactics used by this pest

Table 1. Number of egg batches of *T. pityocampa* collected (*N*)/plot, average (± SEM) of egg batches per tree and estimation per hectares for three life cycles of PPM.

Plots	Life cycle	N	Mean ± SEM^a	SD^b	V.C.^{c}	Eggs/ha^e
	I	289	8.3 ± 0.4	6.3	76.45	16514.3
M1	II	278	7.9 ± 0.3	5.3	66.05	15885.7
	III	843	24.1 ± 0.7	21.3	88.38	48171.4
			$F_{(102,2)} = 17.19\ (P < 0.001)^d$			
	I	43	1.2 ± 0.3	1.9	161.69	2457.1
M2	II	44	1.3 ± 0.4	2.4	187.39	2514.3
	III	152	4.3 ± 0.4	4.9	111.96	8685.7
			$F_{(102,2)} = 10.15\ (P < 0.001)^d$			
	I	155	4.4 ± 0.4	5.5	123.11	8857.1
M3	II	148	4.2 ± 0.4	5.4	127.49	8457.1
	III	212	6.1 ± 0.4	7.4	121.91	12114.3
			$F_{(102,2)} = 0.93\ (P = 0.40)^d$			
	I	33	0.9 ± 0.2	1.1	121.78	1771.4
MN	II	38	1.1 ± 0.2	1.1	98.32	2171.4
	III	189	5.4 ± 0.3	3.9	73.42	10800.0
			$F_{(102,2)} = 37.90\ (P < 0.001)^d$			

Explanations: [a] Standard error of the mean egg batches; [b] SD: Standard deviation; [c] V.C.: Variation coefficients (%); [d] ANOVA test; [e] estimation of egg batches number per hectare.

insect to survive in semi-arid climatic conditions and inform on the fecundity potential. The results could allow elaborate a pest management strategy in order to survey and control this pest insect notably at afforestation conditions (Demolin & Rive 1968; Du Merle 1988; Zamoum et al. 2007).

Material and methods

Study area

Afforested sites of Djelfa which are situated 300 kilometers to the South of Algiers and are traversed by the Saharan Atlas range were chosen for investigations of the abundance of PPM. The altitude of the sites is between 1000 and 1300 m a.s.l. and their climate could be considered as part of the semi-arid bioclimate with cold winter. The annual average of thermal amplitude range is 21.6 °C which indicates a continental climate. Precipitation average is approximately 300 mm/year. The sirocco phenomenon which is characteristic of this locality consists of hot and dry winds lasting, on average, 13 days/year in summer. The Moudjebara afforested area is the experimental zone where more than 100,000 ha were planted with *Pinus halepensis* Miller. Its plantation density equals to 2,000 trees/ha arranged in rows and pine trees height varies between 0.50 and 4 m.

Delimitation of plots and sampling trees

Three successive life cycles of the PPM were studied: cycles I and II correspond to the increasing population density and cycle III for the outbreak. Four plots with 10 ha each were selected in the afforested area of Moudjebara (M1, M2, M3 and MN). Sampling of 35 trees per stand was carried out on a linear transect between 400 to 500 m in length avoiding the roadside effects. These trees were over 20 years old and up to 4 m in height.

Observations and sampling

To observe the variations of egg batches during the three life cycles of PPM in each stand, we counted egg batches at the end of the adult emergence period in the last week of October. Egg batches were collected and kept separately in glass tubes (8 × 1 cm), which were closed with cotton at both ends.

Before sampling, we noted the height of egg batches from the ground, their orientation and support (needles or branches) chosen by females. We studied the relationship between egg number and egg batch length in each plot and life cycle I ($n = 768$ egg batches), II ($n = 652$) and III ($n = 1302$). We removed the scales in the laboratory from each egg batch and measured its length and counted eggs and rows; we used a linear adjustment for the descriptive model.

Additionally, rearing of female pupae was initiated from materials collected at a site in Moudjebara. When adult females emerged, forewing length and weight immediately after emergence were measured in both, those with annual diapause (year n) and with biannual one (year $n+1$). By dissecting the females, the numbers of eggs contained in ovaries were counted. This aimed to determine whether there is a relationship between the measured parameters and potential fecundity of females, which corresponds to eggs number that may be laid by the females under optimal conditions.

Results

Egg batches numbers in studied plots

The variation coefficient (V.C. $>$ 50%) of abundance of PPM egg batches per tree demonstrated high annual and plot variations. The results show that a major difference in density of egg masses was observed in cycle

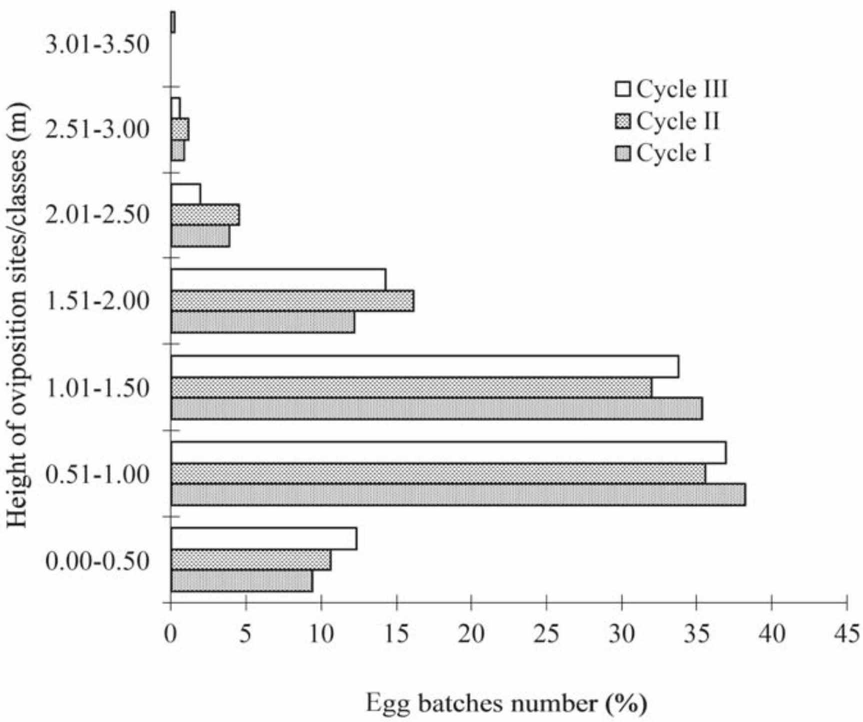

Fig. 1. Distribution of egg batches rates of *T. pityocampa* according to their height above the ground, in M1 plot for the life cycle I ($n = 289$), II ($n = 278$) and III ($n = 843$).

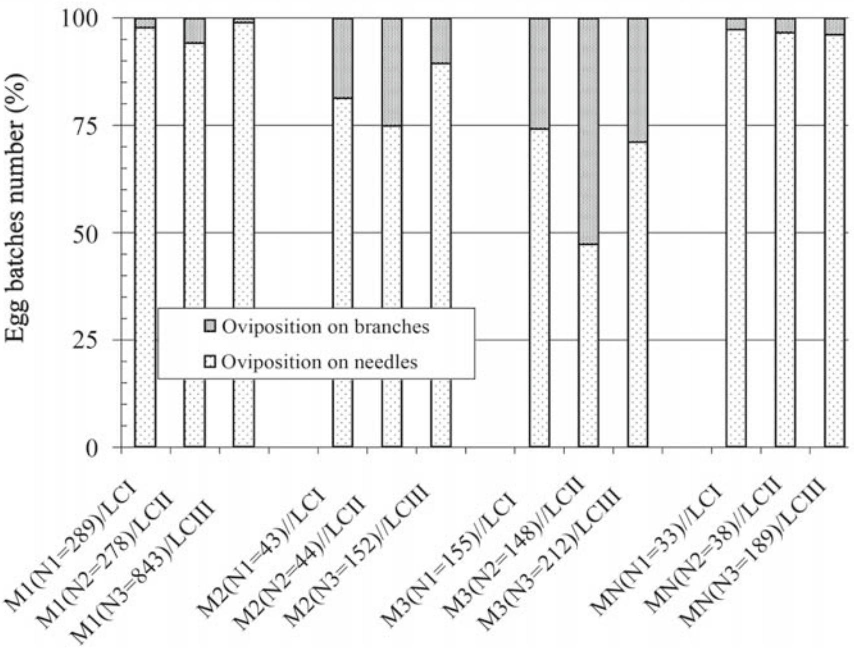

Fig. 2. Annual comparison of oviposition sites selected by adult *T. pityocampa* females for each plot during the three studied life cycles of PPM (LC I, LC II and LC III).

III and that there was a yearly increase in egg batch numbers in different plots (ANOVA test; $P < 0.05$) except in M3 where the progress was slowed down during life cycle II (Table 1).

Choice of the support, orientation and egg laying sites
It seems that adult PPM females do not choose sites on the tree top, but on parts of intermediate height, which are full of foliar biomass. In fact, up to 80% of egg batches are concentrated between the height of 0.5 and 1.5 m (Fig. 1). Distribution of egg deposition sites was related to their height above the ground and differed between years ($\chi 2 = 86.34$; df = 8; $P < 0.001$).

A comparative study of egg batch rates deposited on needles and twigs, respectively, showed a variability between plots and years (ANOVA test; $P < 0.05$)

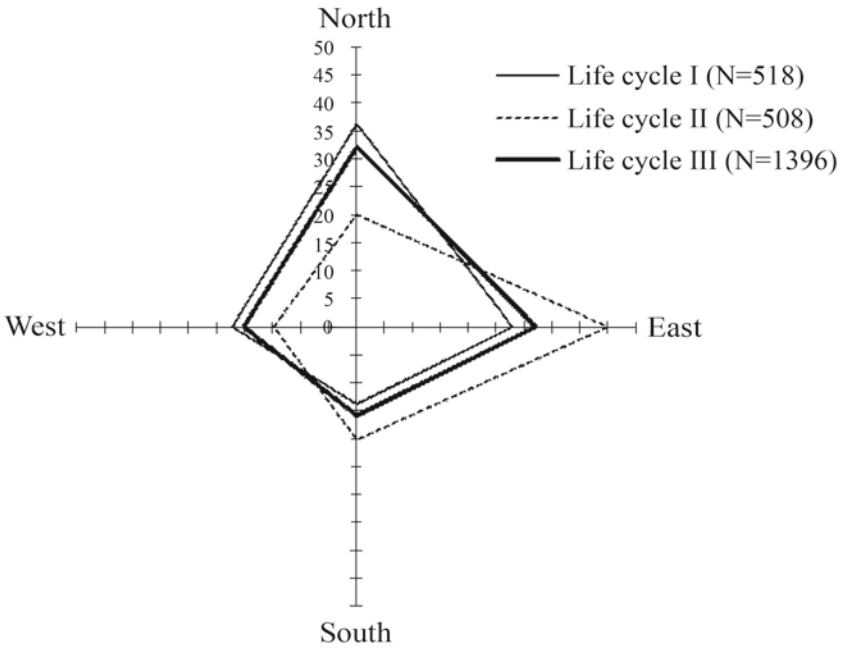

Fig. 3. Geographical positions rates related to the oviposition sites of *T. pityocampa* in Moudjebara.

Table 2. Limit values (maximal/minimal) and means (± SEM) of eggs per egg batches of *T. pityocampa* collected in Moudjebara from each plot and life cycle of PPM.

Plots	Life cycle	N	limit values	Mean (± SEM)	SD[a]	V.C.[b]
M1	I	237	210-18	121.5 ± 2.5	38.3	31.6
	II	119	212-33	107.5 ± 3.2	35.3	32.9
	III	758	246-14	133.6 ± 1.3	36.9	27.6
		Anova	$F_{(1111,2)} = 30.65$ ($P < 0.0001$)			
M2	I	41	186-16	107.8 ± 6.2	39.9	37.0
	II	41	184-45	114.5 ± 6.6	42.1	36.8
	III	152	218-27	135.2 ± 3.0	36.8	27.2
		Anova	$F_{(231,2)} = 10.85$ ($P < 0.0001$)			
M3	I	105	203-14	104.3 ± 3.7	37.6	36.1
	II	128	176-19	113.7 ± 2.7	30.6	26.9
	III	211	228-14	130.1 ± 2.5	35.6	27.4
		Anova	$F_{(441.2)} = 21.64$ ($P < 0.0001$)			
MN	I	33	252-76	160.0 ± 6.8	39.2	24.5
	II	35	223-84	156.9 ± 6.5	38.4	24.5
	III	188	254-11	160.5 ± 3.6	48.9	30.5
		Anova	$F_{(253.2)} = 0.08$ ($P = 0.91$)			

Explanations: [a] SD: Standard deviation; [b] V.C.: Variation coefficients (%).

except for M3 ($F_{(1,4)} = 5.59$; $P = 0.07$). The mean percentage of egg batches deposited on branches exceeded 15% in all plots with a maximum rate reaching 25.8, 52.7 and 28.7%, respectively, for each life cycle of the PPM (Fig. 2).

While average geographical orientation of egg batches on sample trees to the east was 33.7% for the three studied life cycles, other orientations were shared almost equally by the rest of the egg batch population (ANOVA test $F_{(2,9)} = 2.26$; $P = 1$) (Fig. 3).

Estimated number of eggs

ANOVA (F) shows that the average number of eggs per batch differed from year to year for each stand, except in MN, where an insecticide treatment was performed during cycle II (Table 2). The average number was around 130 eggs for the three life cycles: it was low in cycles I and II and increased with density of egg batches in all plots in the life cycle III (i.e., outbreak period).

Table 3. Relationship between each population of *T. pityocampa* with the same number of eggs rows and the eggs number and length of eggs batches.

Number	Egg batches support	Rows Number	Regression equations	R^{2c}
28	N[a]	5	y = 47.61x – 9.49	0.91
1002	N	6	$y = 57.69x - 7.15$	0.96
1136	N	7	$y = 66.15x - 9.14$	0.94
166	N	8	$y = 71.65x - 7.47$	0.91
30	B[b]	9	$y = 62.21x - 15.13$	0.68
85	B	10	$y = 86.18x - 10.04$	0.89
118	B	11	$y = 90.42x - 4.66$	0.88
93	B	12	$y = 97.42x - 5.40$	0.82
34	B	13	$y = 112.31x - 21.96$	0.85
30	B	14	$y = 99.27x - 4.51$	0.71

Explanations: N[a]: egg batches from needles; B[b]: egg batches from a branches; R^{2c}: All the determination coefficients are significant ($P < 0.01$).

Table 4. Relationship between the number of eggs and some measured biological characters of adult *T. pityocampa* females emerged in the laboratory.

Biological characteristics	Regression equations	R^{2a}
Forewing lenght (mm)	$y = 196.3x - 265.2$	0.71
Fresh weight adults[b] (g)	$y = 478.3x - 2.1$	0.70
Weight pupae (g)	$y = 348.6x - 24.7$	0.64

Explanations: [a] Determination coefficient (degree of freedom = 97; $P < 0.01$); [b] in gram (g).

Relationship between number of eggs and length of egg batches

The number of rows in egg batches was generally between 5 and 8 in case of egg batches on pine needles and between 10 and 15 for those around branches; the former measured between 0.3 ± 0.04 and 4 ± 0.08 centimeters (± S.E.) in length and the later between 0.5 ± 0.38 and 3.3 ± 0.37 centimeters (± S.E.).

Determination coefficients (R^2) showed that the length of egg batches was related to the number of eggs deposited on needles but not for those deposited on branches. In fact, a variation of 91–96% and 68–89%, respectively, was observed (Table 3).

Parameters measured for adults and fertility

Comparison between average fecundity during the two studied cycles in PPM females that emerged in semi natural conditions with a biennial diapause at year $n + 1$ after pupation and in those with annual diapause emerging under the same conditions in year n showed a significant decrease (Student test; $P < 0.05$). In addition, for the females that emerged in year n, a significant linear relationship ($P < 0.01$) was found between fertility of individual females and length of their forewing, fresh weight of the adult and weight of pupae, respectively. The measured characters explained 64–71% of the variation in egg numbers in mature females (Table 4).

Discussion

Egg batches abundance variation

Heterogeneity in plots with regards to average abundance of PPM egg batches (± SEM) that varied between 4.3 ± 0.4 and 24.1 ± 0.7 egg batches/tree was observed in the outbreak area. It shows the reproduction potential of PPM populations, which is much higher compared to other pine afforestations in Algeria: 1.24 egg batches/tree in Meftah (near Algiers) and 1.5 in Bouilef (Batna) (Bertella 1987).

The reproduction potential of PPM in South of Algeria depends on several factors. First, prolonged diapause capacity allows the emergence of adults of the same generation over several years, thus limiting the risk of local extinction and increasing the probability of retaining local genetic diversity (Kerdelhué et al. 2009); second, availability and quality of food for caterpillars depends on plantation structure (foliage biomass, height and density of trees) (Battisti 1988; Buffo et al. 2005). Moreover, survival of egg bathes depends on activity of predators (hedgehogs and birds) and lastly, on hail frequency and intensity (Zamoum 1998). The hail frequency was, on average, 3 days/year in late summer and autumn, causing a loss of up to 19% of egg batches in Moudjebara (Zamoum & Demolin 2004, 2005).

It appears that the highest abundance of egg batches was observed in M1 which seems to prove that this plot was at risk for permanent infestation by the PPM. As M1 is a slope located between the *P. halepensis* natural forest of Djellal and the Moudjebara afforested area, it might constitute an ecological protective barrier against dispersion of adult females in the Djellal forest. This sylvicultural tactic of controlling this insect pest has been noted by Demolin (1969) and Longo et al. (1989).

Habitat selection for oviposition

In our study, the choice of oviposition sites was limited by the exclusive presence of the *P. halepensis* host. Sites for deposition of egg batches are located at the periphery and in the middle part of pine; it demonstrates the importance of foliage biomass in these levels of trees. The highest pine trees which are situated at the border and those on the top and in the middle of the mountain constitute favorite habitats to oviposition. This choice is not only due to the "silhouette" of these trees (Demolin 1969; Zamoum 1998; Zovi et al. 2005), but also to the presence of volatile secondary metabolites in host trees (Tiberi et al. 1999; Hillbur et al. 2005). In these preferred habitats, the PPM is permanently and inconspicuously present during decreasing population densities. These factors influence the recurrence of PPM at Moudjebara and the egg batches dispersal moves from the border to the inside of the plot and from lower to higher altitudes.

The choice of branches as oviposition sites may be related to defoliation intensity during precedent development cycles. As PPM females try to find ideal needles support in vain, they opt for branches, for instance M3 and M4. Indeed, the optimal diameter of needles must be between 1.6 and 2 mm permitting to females to deposit eggs easily (Demolin 1969). This, however, involves an exigent physical support, because, on one hand, the impulse during egg laying becomes more and more strong as the spermatheca fills. On the other hand, females in Moudjebara can not oviposit under a temperature of approximately 28 ℃ at the onset of dawn (Zamoum 1998). Otherwise, PPM females can also gather 3, 4 or 5 needles and deposit eggs around them randomly, without scales at the extremities or on certain central mass parts. Oviposition can sometimes be on 2 or 3 parts of gathered needles. Evidently, eggs not protected with scales can be attacked by egg parasitoids (Zamoum 1998), hamper embryogenesis and become highly sensitive to thermal stress (Milani 1990).

Dominant orientation of egg batches to the East in Moudjebara may be due to the influence of relief on dispersion after mating. In fact, two mountainous formations are present; one of them is situated in East the second in South of Moudjebara. Positive phototropism which is linked to dawn can influence females to lay intensively in this period (Zamoum et al. 2006).

Particularities of fecundity potential

The average number of eggs in PPM batches observed during the three studied life cycles in Moudjebara was 126, which is far lower than already observed in Algeria: 169 in Meftah (Algiers), 176 in Bousaada (Bertella 1987), up to 256 in North of Morocco (Questienne & Miermont 1978), almost 200 in Corsica (France) (Geri 1980), 184 to Peloponnesus in Greece (Schmidt & Douma-Petridou 1989), 231 the North of Italy (Tiberi 1978) and 255.9 in the South Italy (Longo et al. 1989) and finally between 16 to 322 in *Pinus* forest in Portugal (Santos et al. 2013). Size of individual moths is linked to fecundity potential variations and to the existence of a probable geographic cline related to latitude and longitude (Pimentel et al. 2010). This would be worth to confirm as that would permit adaptation to local trophic and climatic conditions.

It is necessary to mention that in favorable conditions for larval development, the potential fecundity of PPM would be 340 eggs (Demolin 1970). Besides these factors linked with individual and genetic difference (Wellington 1957; Foltz 1972), other lepidopteran forest species which are in connection with the trophic aspect may also influence eggs number variations in PPM (Battisti 1988; Markalas 1989; Zamoum 1998).

In general as well as in the studied populations in the North of the Mediterranean region, interannual fecundity variations can be an indicator of the population density of the PPM. This shows that fecundity rate is low during the increase and decrease periods of the population dynamics, in biennial diapausing females, in populations which developed in defoliated areas in previous year, and in those under constraint climatic conditions at the northern limit range of PPM (Battisti et al. 2006) and at the southern one.

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