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Life-cycles and biological features of eggs predators of *Lymantria dispar* (Lepidoptera: Lymantriidae) in the Mamora cork oak forest, Morocco

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Abstract. The gypsy moth oophagous predator guild in the Mamora forest is an assemblage of many species whose succession in egg masses enhances the exploitation of this food source. Life history, biological features and trophic capacities of predator species are described from field observations and laboratory rearing. Extreme diversity of diets, capacity to resist prolonged fasting and extended larval development with extra-instars enable them to survive on the cork oak when gypsy moth egg masses are absent. The 1986–1990 gypsy moth outbreak occurred in a forest part where unhealthy cork oaks are common. By providing abundant shelter for numerous arthropods these trees are beneficial to the oophagous predators which find there various and abundant food sources. This probably explains why egg predator activity in the infested area rapidly increased so that the pest outbreak collapsed.

INTRODUCTION

In the Mamora forest, near Rabat, Morocco, oophagous predators regularly account for 25% egg mortality of the gypsy moth *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) but in some years these same predators may destroy as much as 90% (DeLépiney, 1930; Chakir & Fraval, 1985; Villemant & Ramzi, 1995). In July, gypsy moths lay eggs in several layers, forming a compact cluster covered with hairlike scales from the female's abdomen. Egg masses remain 9 months on the tree trunks before hatching. During this period, predators consume eggs but cause even more damage by foraging and disrupting the egg masses, increasing in this way their susceptibility to other mortality agents. Fragments of disrupted egg clusters are blown down by wind or washed away by rain, while underlying eggs still on the bark are more easily parasitized by *Ooencyrtus kuvanae* (Howard) (Hymenoptera: Encyrtidae). Eggs fallen to ground die, preyed on by ants or various predators (Villemant & Fraval, 1992).

Despite a regularly recorded impact during several decades, the oophagous predator complex of gypsy moth in Morocco remained incompletely known (Hérard, 1979; Chakir & Fraval, 1985). Beginning in 1986 when a localised gypsy moth outbreak started after a long latency period in the north-western part of the forest (Fraval et al., 1988), we took surveys of egg arthropod fauna to obtain precise details concerning the number of species involved in the egg predator complex. By laboratory rearing on cultured gypsy moth egg masses we determined the life-cycle and the number of generations per year of most of the species. We also investigated what other food sources outside of gypsy moth egg masses enable them to survive on the oaks when the pest is absent.

MATERIAL AND METHODS

Faunistic sampling

Between 1986 and 1990, density of gypsy moth egg masses reached high levels (450 to 10,000 per ha) only in the north-western part (1,000 ha) of the Mamora forest, near Kénitra (Villemant & Ramzi, 1995). From 1987 to 1989, between July and March, more than 60 egg masses were collected each month in the most infested zone, in order to obtain living individuals of predators and to evaluate their damage. Two hundred old egg masses were also collected, each year in April and May, to identify the fauna remaining inside after egg hatching. At most, three egg masses were collected on the lower strata (up to 2,5 m above the ground) of each tree. Each egg mass was pulled away by scraping with a knife, and isolated in a small bottle. Before taking the sampling, the presence of *O. kuvanae* emergence holes as well as the presence of any predator species (ants, notably) and their specific damages were recorded. In the laboratory, egg masses were kept at 4°C before being individually inspected under a binocular microscope to extract arthropod fauna. Since 1988, the pest population has nearly disappeared as a result of the combined impact of egg predators and larval parasitoids in the eastern part of the infested area (Villemant & Ramzi, 1995). In order to inquire about living places and feeding habits of the egg predators away from the egg masses, we regularly inspected cork oak trunks of this zone during the two following years. About 13% of the trunks have cavities and 46% more or less large dehiscent cork flaps. Each month we also collected samples of organic matters accumulated under bark flaps (4 samples per month) or in trunk cavities (2 samples per month). Samples, obtained from separate trees, were isolated in large plastic bags. Their fauna, extracted in the laboratory by using Berlèse funnels, was kept in alcohol and sorted under a binocular microscope.

Culturing egg predators

Egg predators were reared at room temperature. Humidity was maintained by moistening a strip of filter paper placed in the rearing containers, as in the laboratory culture of dermestids and other household pests (Blake, 1961; Arbogast & Van Byrd, 1981; Fleming & Jacob, 1986). Suspected egg predators were cultured first on laboratory-reared gypsy moth egg masses so that we could select the species which eat healthy gypsy moth eggs. The characterisation of larvae, traces (larval skins or fecal pellets) and specific damage was made after identification of emerged adults.

From 1988, 9 species were cultured on a large scale on gypsy moth egg masses obtained in laboratory according to Fraval (1989). Except *Dermestes lardarius* whose neonate larvae are able to gnaw the chorion of healthy eggs, the other species were reared on egg masses starting with the third instar. *D. lardarius*, *Aglossa caprealis* and *Tenebroides maroccanus* were placed in large transparent polyethylene boxes (24 × 18 × 10 cm) and the others species in smaller ones (10 × 7 × 2.5 cm). First to third instar larvae were fed with the food diet which resulted in the lowest mortality level: grain of wheat for *T. maroccanus*, dead gypsy moth neonate larvae for *A. caprealis* and pollen for the dermestids. As for *Dasytes terminalis*, which was not mass cultured, last instar larvae of *T. maroccanus* and *D. lardarius* need to penetrate a piece of cork or any other woody matter to pupate.

To evaluate the capacity of egg predators to grow and reproduce on other organic material, third instar larvae hatched in the laboratory were also placed on various other potential foods: egg masses sterilized by high temperatures, dead gypsy moth pupae and adults, wheat and pollen. 30 larvae of a given species were put together in a transparent polyethylene box with a given food medium. Because of the risk of cannibalism, *T. maroccanus* larvae were isolated three by three in large plastic boxes. Referring to the bibliography (Delobel & Tran, 1993), all of the food diets were tested for *Trogoderma meridionalis* and the *Anthrenus* species, excepting *A. minutus* and *A. delicatus* because of their insufficient number. *D. lardarius* and *A. caprealis* were only fed with dead moths and sterilized eggs and *T. maroccanus* with corn, as suggested by DeLépiney (1930).

Beginning in July 1989, 30 or more larvae of each species and generation were individually cultured, from the third instar, on gypsy moth eggs. Each larva was isolated in a small cylindrical polyethylene box (3 cm in diameter × 1 cm high), either on laboratory-reared egg masses, or on dehaired eggs which were glued with Arabic gum to discs of Bristol paper. *D. lardarius* larvae were only reared on egg masses. In the case of *A. caprealis* larvae, which enclosed the eggs in their silk net, the dehaired eggs were not glued on paper. The viability of the eggs mechanically dehaired by a vacuum device similar to the model of Tardif & Secrest (1970) was proved by Fraval et al. (1981). Examinations of the larvae placed on dehaired eggs were made every 3 days in winter and every day in the other seasons to record any moulting. Larvae reared on egg cluster often excavate it and moult inside, so that their instar number could be determined only by counting the moulting skins after adult emergence. Predator larvae which had not yet pupated when the moths hatched were fed with sterilised eggs until new egg masses could be obtained.

Fecundity was established by counting eggs laid by mated females. Each couple was isolated in a polyethylene box and provided with pollen (*Anthrenus* spp., *T. meridionalis*), egg masses (*D. lardarius*, *T. maroccanus*) or sugar and water (*A. caprealis*). Sexes of *A. delicatus* and *T. maroccanus* being indistinguishable, adults were paired by isolating a small individual with a large one in a box. It appeared necessary to supply *T. maroccanus* females with a piece of cork to initiate egg laying.

TABLE 1. Gypsy moth egg predators in the Mamora forest and their occurrence, between July 1987 and March 1989, in/on more than 10% (***), 1 to 9% (**), or less than 0.3% (*) of the collected egg masses.

Coleoptera: Dermestidae	
Dermestes lardarius (L.)	***
Attagenus trifasciatus (F.)	*
Anthrenus (*Nathrenus*) sp.	**
A. verbasci (L.)	**
A. minutus Erichson	**
A. pimpinellae delicatus Kiesenwetter	**
A. vladimiri Menier et Villemant	***
Trogoderma versicolor meridionalis Kraatz	***
Coleoptera: Trogossitidae	
Tenebroides maroccanus (Reitter)	***
Temnochila coerulea Olivier	*
Coleoptera: Cleridae	
Opilo domesticus (Sturm)	*
Coleoptera: Melyridae	
Dasytes terminalis (Du Val)	***
Coleoptera: Tenebrionidae	
Akis tingitana Lucas	**
Lepidoptera: Pyralidae	
Aglossa caprealis (Hübner)	***
Lepidoptera: Tineidae	
Niditinea fuscipunctella (Haworth)	**
Hymenoptera: Formicidae	
Aphaenogaster senilis disjuncta Santchi	**
Crematogaster scutellaris (Olivier)	***

RESULTS

Seventeen insect species have been observed feeding on gypsy moth eggs and all of them, except the ants, were fed on gypsy moth egg masses in laboratory (Table 1). Keys of all predator species (adults and larvae) and descriptions of their eggs and fecal pellets have been published (Villemant & Fraval, 1992). A new dermestid, *Anthrenus vladimiri*, was described (Menier & Villemant 1993). Identification of *Anthrenus* (*Nathrenus*) sp. as *A. exilis* Mulsant & Rey (1868) could not be confirmed as the type of this species was lost (V. Kalík, in. litt.). Mediterranean specimens of *Trogoderma versicolor* Mutchler & Weiss belong to the subspecies *meridionalis* Kraatz, which could be a synonym of *T. inclusum* Leconte (Delobel & Tran, 1993). *Akis tingitana* was previously misidentified as *A. bacarozzo* Schrank by Hérard & Fraval (1980).

Damage period and impact

Field and laboratory observations concerning the presence and activity of each predator species in egg masses are summarised in Fig. 1. Many predators do not remain for long in a given egg mass but their attack is often detectable by the presence of their moulted skins or fecal pellets, so that their attack-frequency could be estimated.

D. lardarius attack began when the gypsy moths started laying and ended in August. During this period it damaged about 11% of the egg masses in 1987 and 32% in 1988. Other dermestids larvae were observed all along the

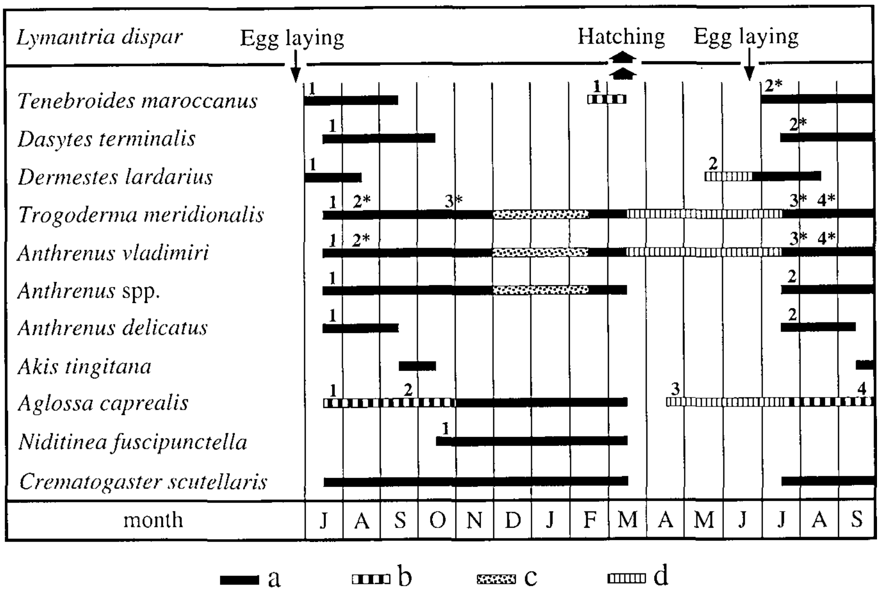

Fig. 1. Evidence of predators gypsy moth egg masses in the Mamora forest. Predation period (a) of most individuals, (b) of only a few individuals; (c) diapause period within egg masses, (d) feeding period on old egg masses. The number (1–4) indicates the generation rank of the individuals. An asterisk indicates when long-living individuals of previous generations are still present in egg masses.

L. dispar egg stage. *T. meridionalis* attacked respectively 14 and 7% and *A. vladimiri* 16 and 9% of all the egg masses collected in 1987–88 and 1988–89. Other *Anthrenus* species were more occasional, their attacks never exceeding 5%. Except a few individuals collected later, *T. maroccanus* larvae were found between July and September, during which months they damaged 25% of the egg masses in 1987 and 36% in 1988. While less than 6% were attacked by *A. caprealis* during the summer, egg masses suffer from December onwards conspicuous damage by old larvae which destroyed about 24% of them each year. *D. terminalis* larvae attacked 12 to 18% of the egg masses between July and October and those of *Niditinea fuscipunctella* 2 to 9% from October to March. Adults of *Akis tingitana* were seen consuming egg masses every year but only during a few weeks in late summer.

TABLE 2. Variability of total development duration (egg to adult) and larval instar number of predator species reared, from the third instar, on gypsy moth egg masses (a) or dehaired eggs glued on paper disk (b).

Egg predator species	Generation rank	Egg diet	Reared L3 larvae number	Development duration (min-max days)	Larval instar number (min-max)	Emerged adults number	Sex ratio Y/X
Tenebroides maroccanus	1/1	a	36	95–361	4–6	31	14/17
	1/1	b	36	93–362	4–6	33	17/16
Dermestes lardarius	1/1	a	79	33–72	5–7	68	37/31
Anthrenus delicatus	1/1	a	23	88–152	5–7	23	–
	1/1	b	35	82–145	5–7	23	–
Anthrenus minutus	1/1	a	26	285–343	6–8	24	12/12
	1/1	b	21	288–351	6–9	19	6/13
Anthrenus (*Nathrenus*) sp.	1/1	a	33	362–381	7–9	32	16/16
	1/1	b	33	365–375	7–12	30	17/13
Anthrenus verbasci	1/1	a	23	318–360	8–10	16	8/8
	1/1	b	33	317–704	8–15	24	13/11
Anthrenus vladimiri	1/2	a	26	76–440	5–15	24	11/13
	1/2	b	35	77–451	5–15	33	17/16
	2/2	a	35	283–709	8–15	27	12/15
	2/2	b	32	282–683	8–15	25	14/11
Trogoderma meridionalis	1/3	a	26	58–849	5–19	22	11/11
	1/3	b	38	57–798	5–19	32	18/14
	2/3	b	36	64–775	5–18	24	14/10
	3/3	b	26	268–1047	7–21	8	5/3
Aglossa caprealis	1/2	a	39	72–85	6–7	29	12/17
	1/2	b	34	73–95	6–8	25	15/10
	2/2	b	42	224–313	7–9	24	10/14

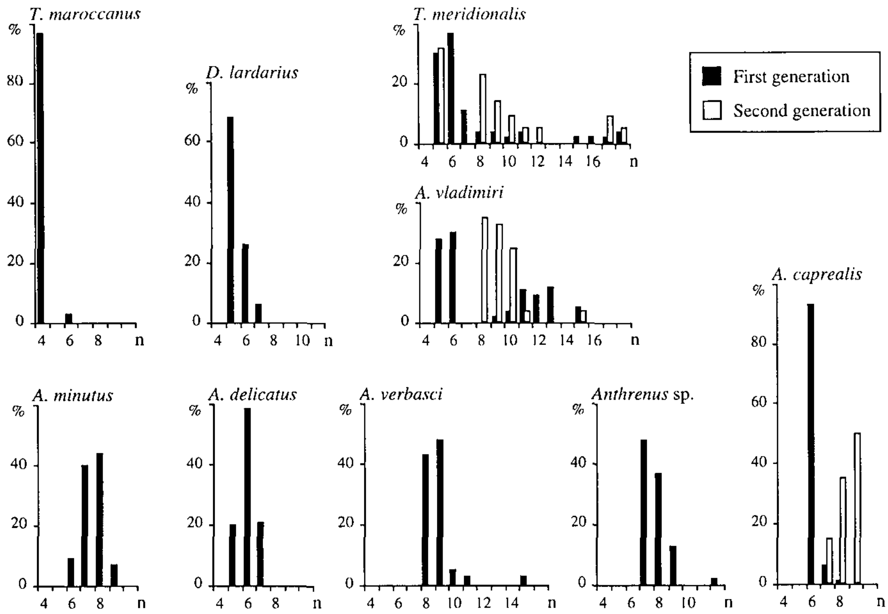

Fig. 2. Frequency distribution (%) of the larval stage number (n) of gypsy moth egg predators.

Ants, whose activity only slows down in winter, do not seem to be attracted by unparasitized egg masses. We often saw them, mostly *Crematogaster scutellaris*, detaching individual parasitized eggs from egg masses without disrupting their cohesiveness. In both years, from September onwards, more than 80% of the collected egg masses showed *O. kuvanae* emergence holes, and more than 40% appeared to be attacked by ants. However, predation by ants was not precisely estimated because their damage cannot be detected when egg masses are disrupted by oophagous predators.

Life-cycle and biological features

Rearing results are presented in Tables 2–4 and Fig. 2. Table 5 sums up the predator's numbers obtained in egg masses between 1987 and 1989 as well as in the different samples collected on oak trunks in 1989 and 1990. Owing to sample size variability as well as heterogeneous predator distribution, these data only inform about the relative frequency of the species in each examined oak habitat. Analysis of laboratory data completed by field observations will be presented species by species.

TABLE 3. Fecundity of mated females of predator species individually reared in laboratory.

Predator species	Mean fecundity	± S.E.	Female number
Tenebroides maroccanus	62.8	± 8.3	4
Dermestes lardarius	30.3	± 4.1	9
Anthrenus minutus	20.3	± 3.4	8
Anthrenus (Nathrenus) sp.	24.1	± 6.7	16
Anthrenus verbasci	67.1	± 20.4	11
Anthrenus vladimiri	28.8	± 6.7	8
Trogoderma meridionalis	68.4	± 32.7	27
Aglossa caprealis	270.0	± 87.5	24

Tenebroides maroccanus

Most of the larvae develop in 4 instars and groove the cork to pupate, 3 months after hatching. A few individuals however, prolong their development (6 instars) until the following year (Table 2). Adults emerge between August and September but, as long-living larvae, remain inactive in cork excavations during the winter months. In spring, each female lays separately in cork cracks about 60 eggs, the egg laying period lasting 2 to 3 months (Table 3). From July to September, larvae excavate the cork as well as egg masses laid on it. Often an excavation in the cork begins just below the egg mass and the larva escapes inside when disturbed. Deserted egg masses are recognisable by the presence of cork shavings and typical fecal pellets. In laboratory *T. maroccanus* was fed with egg masses and wheat (Table 4). Development was similar on the two diets and few of the 56 surviving larvae showed a prolonged life: 2 were fed with eggs and 4 with wheat. Carnivorous habits of adults and larvae on living arthropods were noticed in the field and in the laboratory. On oak trunks, they find prey by moving in cork excavations and under bark flaps (Table 5).

Dasytes terminalis

Development may last either 1 or 2 years. In autumn, larvae vacate egg masses and penetrate the cork in which they remain inactive during the winter months. Most of them pupate in spring, and adults, which emerge between March and April, feed on cork oak flowers. Long-lived larvae leave cork excavations in late spring in which period they may excavate new egg masses. Larvae also feed on active living arthropods and were observed running on oak trunks or in various cork shelters (Table 5).

Dermestes lardarius

In the Mamora forest, this species has only one generation per year and 5 to 7 larval instars which last 1 or 2

TABLE 4. Survival number of predator species reared, from the third instar, on five food diets (30 larvae / diet in the same container, except for *T. maroccanus* larvae which were reared in group of three). (*) egg laying and development of the following generation without any other food supply; (–) untested diet.

Egg predator species	Healthy egg masses	Sterilized egg masses	Dead gypsy moths	Wheat	Pollen
Tenebroides maroccanus	28	–	–	28*	–
Dermestes lardarius	30	22	23	–	–
Anthrenus delicatus	28	24	25	–	27*
Anthrenus minutus	24*	22*	25*	–	25*
Anthrenus (Nathrenus) sp.	28*	28*	27*	28*	28*
Anthrenus verbasci	28*	29*	26*	23*	29*
Anthrenus vladimiri	26	20	21	18	28*
Trogoderma meridionalis	30*	29*	24*	30*	30*
Aglossa caprealis	23	20	24	–	–

months (Table 2). Pupation occurs in the cork. Adults emerge mostly during June and July but remain inactive till March–April. Locally, they were observed in winter, gathered under dehiscent bark flaps. Each female lays about 30 eggs (Table 3), in clusters of 2 to 6, within animal fragments in cork shelters or even in hatched *L. dispar* egg masses in which neonate larvae were observed in spring (Table 5). In the laboratory, larvae developed on dead gypsy moths and sterilized egg masses. Their mortality, however, was significantly greater on both these diets than on healthy egg masses (χ^2: $p < 0.001$) suggesting that water provision was insufficient (Table 4). On oak trunks, in addition to eggs, the larvae eat preferably recently dead gypsy moth pupae or adults, and especially females whose abdomen still contained eggs. Moreover, we observed on one occasion a larva attacking an egg mass still being laid by a moth. *D. lardarius* adults and larvae are mostly encountered under bark flaps but also in bird nests hidden in trunk cavities (Table 5). They are especially numerous on trunks when *L. dispar* remains are abundant. They were also observed in thousands in the cattle or dog carcasses frequently lying in the forest.

TABLE 5. Total number (larvae and adults) of living predators collected in egg masses and oak trunk shelters. NE – gypsy moth egg masses; HE – hatched egg masses; BF – bark flaps with dead arthropods matter; TC – trunk cavities with various organic matter. The adult number is given between brackets.

Habitats	NE	HE	BF	TC
Sample number	1436	400	96	48
Tenebroides maroccanus	43	0	8 (5)	2
Dasytes terminalis	18	2	10	0
Dermestes lardarius	14	6	37 (21)	7
Trogoderma meridionalis	101	17	21	1
Anthrenus vladimiri	136	72	5	0
Anthrenus minutus	5	3	21	0
Anthrenus (Nathrenus) sp.	12	2	17	1
Anthrenus verbasci	4	1	2	3
Anthrenus delicatus	8	1	31 (29)	0
Akis. tingitana	1	0	24 (24)	47 (47)
Aglossa caprealis	84	23	48	11
Niditinea fuscipunctella	12	0	2	5
Crematogaster scutellaris	138 (138)	0	145 (145)	21 (21)

Trogoderma meridionalis and *Anthrenus vladimiri*

Most individuals of the same birth cohort (born at the same time) complete larval growth in 2 to 4 months (5 to 9 instars). A second generation appears during the same year, and even a third in the case of *T. meridionalis*. A few long-living larvae of the first generation and more of the following ones, enter prolonged diapause in egg masses before the winter and become active again in the spring. Their life-cycle may last 1 or 2 years and their larval development may reach 15 (*A. vladimiri*) to 21 (*T. meridionalis*) instars. Larval mortality however increases with development duration (Table 2, Fig. 2). Long-living larvae provide very small yet reproductive adults.

Feeding is not necessary for *T. meridionalis* egg laying. In the laboratory, females laid 30 to 200 eggs according to their body size. A *A. vladimiri* female laid about 30 eggs but only when provided with pollen (Table 3). Both species were mass-reared on pollen. Continuous rearing of *T. meridionalis* on tough food source, such as healthy or dry eggs, or wheat, which young larvae are enable to gnaw, is facilitated by their capacity to eat small organic fragments or by consuming their own parents, dead after egg laying in the rearing containers. *A. vladimiri* larvae showed significantly lower mortality levels when fed on pollen or egg masses than on wheat (χ^2: $p < 0.001$). Their survival was lower on dead gypsy moths or sterilized eggs (Table 4). On all tested food diets, several larvae of both species showed a prolonged development. *T. meridionalis* may endure prolonged starvation. From July 1988, 10 larvae were placed together in an empty rearing box and survived during six month in spite of the lack of food. During this period the starving larvae did not exhibit any cannibalistic propensities and underwent several retrogressive moulting. In January, the larvae were fed again with eggs and, while two of them died, six developed to adults in summer of the same year and two prolonged their development until the following year.

In the forest, both species were mostly collected in *L. dispar* egg masses, two or more individuals sometimes being encountered in the same egg mass. In early spring, long-living larvae were found in old egg masses where they ate dead embryos that remain after gypsy moth hatching (Table 5). *T. meridionalis* larvae were also collected in dried-mud nests filled with spiders, which sometimes were built under oak branches by the wasp *Sceliphron spirifex* (L.) (Hymenoptera: Sphecidae).

Anthrenus spp.

The life-cycles of *Anthrenus* sp., *A. minutus* and *A. verbasci* last about one year except for a few *A. verbasci* individuals which develop in 2 years and reach 11 to 15 larval instars (Table 2, Fig. 2). Larvae remain inactive in egg masses or cork shelters during the winter months (Fig. 1). *A. delicatus* develops in 3 or 4 months; the adults emerging in summer remain inactive gathered under cork flaps until the following spring. While no oviposition was obtained from paired *A. delicatus* adults, fecundity of the other species reached 20–25 (*A. minutus*, *Anthrenus* sp.) to about 70 eggs (*A. verbasci*) per female (Table 3). Larvae may survive on sterilized egg masses, dead gypsy moths, wheat and pollen as well as on healthy egg masses. As their neonate larvae eat small organic fragments or their dead parents, all the species have been continuously reared on pollen as well as on the other diets, except *A. delicatus* whose adults never laid egg without feeding pollen (Table 4). Several *A. verbasci* individuals showed prolonged development on the various diets. *Anthrenus* larvae were not often collected in cork shelters (Table 5) while, contrary to *T. meridionalis* and *A. vladimiri*, many adults were observed in spring feeding on the umbellifers which abound in the forest border.

Aglossa caprealis

While the spring generation develops in about 2.5 months, summer generation moths emerge between March and June, 7.5 to 10.5 months after hatching. Egg masses damaged by the old larvae are easily recognizable by the presence of a silk net enclosing eggs fragments and typical fecal pellets. In the laboratory, each female laid separately 120 to 450 eggs (Table 3). With a sufficient water supply, larval survival was the same when fed either with dead gypsy moths, sterilized or healthy egg masses (Table 4). *A. caprealis* larvae were observed in all trunk shelters (Table 5). In summer, old larvae were also collected in the litter (Benhalima et al., 1991). Pupation often occurs under bark flaps in a silk cocoon including various organic fragments. Moths hide during the day in cork cracks. Eggs were observed singly or in groups of 2 or 3, in fragments accumulated under bark flaps, in cork cracks or in scales covering new and old egg masses. Neonate larvae were collected in damaged egg masses as well as in hatched ones where they ate destroyed eggs and *O. kuvanae* pupal skins (Fig. 1).

Niditinea fuscipunctella

Larvae which commonly excavate the bark of cork oak in the Mamora forest (Villemant & Fraval, 1993), may also develop in the organic fragments present under bark flaps or bird nests built in trunk cavities (Fig. 5). Some larvae penetrate into egg masses during the winter months (Fig. 1). According to DeLépiney (1930) they would mostly consume dead eggs or those previously destroyed by another oophagous species. In laboratory, however, most of the larvae collected in the field survived on healthy egg masses and became adults in March.

Akis tingitana

Adults, which usually move on the forest floor, climb the trunks in spring to eat parasitized larvae or dead gypsy moth individuals (Hérard & Fraval, 1980; Villemant, 1989). They were never seen consuming egg masses except during two or three weeks between September and October. Adults caught at this period were placed for 3 months in boxes containing egg masses and cork oak litter. Examination of their fecal pellets under a binocular microscope showed that they ate eggs as well as dead plant matter.

DISCUSSION

The temperate climatic conditions in Atlantic cork oak forests enable the predators to exploit egg masses during the complete 9-month duration of the gypsy moth egg stage. They showed allotrophic capacities, extended larval development with extra instars or prolonged survival of the adults which are adaptive characteristics of species inhabiting unstable environments (Danks, 1992). This is notably the case for many Mediterranean animal species which undergo climatic perturbations and whose host (a plant or an animal highly dependent on a plant) varies unpredictably (Lamotte & Blandin, 1989; Lamotte et al., 1991). These features are common in the stored product pests of which almost all gypsy moth egg predators throughout the world are representatives (Brown & Cameron, 1982; Coulson et al., 1986; Schaefer & Beal, 1996).

Variability of larval instar number

The duration of larval development and the number of larval instars vary across individuals and generations in several of the main predator species, whatever eggs they consumed (egg masses or dehaired eggs) (Fig. 2, Table 2). As a result, adults emerge over a period of several months or even years. Prolonged development was shown for the stored grain pest, *Tenebroides mauritanicus* L. (Candura, 1932). It was well studied among *Trogoderma* and *Anthrenus* species. It seems to be mainly conditioned by environmental factors (diversity, quality and abundance of food supplies, habitat temperature and moisture, intra- and interspecific competition) but also by genetic factors, the development duration varying even among siblings reared under identical conditions (Blake, 1961; Nair & Desai; 1973; Barak & Burkholder, 1977; Elbert & Levinson, 1979). Long-lived individuals, whose growth stopped when the habitat remained unfavorable for a long time, ensure the survival of the species. They often have retrogressive molting and their size and fecundity are lower than average. However, they showed a high dispersal ability which is necessary for discovering more favorable habitats (Blake, 1961; Beck, 1973; Danks, 1983). In the Mamora forest, the most common egg predators are indeed highly effective in discovering egg masses as soon as they are deposited on trunks. The influence of attractive kairomones (e. g. the sexual pheromone produced by the moth females) has not yet been proven; however, field and laboratory observations suggest that it probably does occur. For instance, in July 1985 during the latency period of the pest, 380 egg masses, laid on brown cardboard by laboratory cultured moths, were fixed by nails on cork oak trunks (1 egg mass/tree). All of the 210 egg masses found again in October were disrupted and 30% showed an undeniable predator attack due to the presence of destroyed eggs, larval skins or fecal pellets. Moreover, 52 predator larvae (18 *T. meridionalis*, 16 *A. vladimiri*, 8 *D. terminalis*, 6 *Anthrenus* sp., 3 *A. caprealis* and 1 *T. maroccanus*) were extracted from this sample (Villemant, 1993).

Allotrophic capacities

Oophagous predators showed broad feeding habits but most of them have a basically zoo-saprophagous diet (Table 3). Apart from *D. lardarius*, all dermestids may also survive on oak pollen which often accumulates in bark cracks. Apart from ants, only *D. terminalis* and *T. maroccanus* have typically carnivorous habits; the latter can also consume corn seeds like *Anthrenus* and *Trogoderma* species and even *A. caprealis* (Arbogast & Van Byrd, 1981). Many species are also able to survive prolonged starvation (Beck, 1971).

Between 1987 and 1990, oophagous insect activity contributed to a rapid collapse of the localized *L. dispar* outbreak, preventing its spread to other locations. We established that predators caused major destruction to egg masses laid on large and unhealthy trees which had the highest egg mass densities during the infestation period (Villemant & Ramzi, 1995). Most of these trees have cavities, large bark flaps or galleries of xylophagous insects (*Cerambyx cerdo* L., Coleoptera: Cerambycidae, notably) which provide abundant shelters to both the pest (eggs, larvae or pupae) and its egg predators (Villemant et al., 1991). Bark structure and shelter abundance enabled a great number of arthropods to live in and on the tree trunks so that many egg predators may have been present in the appropriate place before the pest outbreak, because they found other suitable food sources.

Water requirement

Despite the proximity of the Atlantic ocean, the Mamora forest experiences several drought months so that many arthropods of the oak trunk fauna take refuge during summer in lower cavities of the trees or in litter (Lamotte et al., 1991). This may explain why attacks of *A. caprealis* larvae on gypsy moth egg masses are much lower during this period than in winter. Furthermore, consuming eggs may provide the water requirements of certain species. Jacobs & Fleming (1982, 1985) demonstrated that water availability favors egg production in *D. lardarius* and has a marked effect on the larval development of *Dermestes maculatus* Degeer so that heavier adults result. Water requirements might also explain why the *A. tingitana* attack is limited to a few weeks at the end of the drought period.

CONCLUSION

The gypsy moth oophagous predator guild in the Mamora forest is an assemblage of many species whose succession in egg masses enhances the exploitation of this food source. Allotrophic capacities, extended larval development with extra instars enable egg predators to survive in spite of the important temporal variations of the pest density. Extreme diversity of diets and capacity to resist prolonged fasting also enable them to remain on the cork oak when gypsy moth egg masses are absent. Because they are efficient in dispersing and discovering their host, they can attack egg masses as soon as these are laid on the trunks. Furthermore, increases in their populations during the pest outbreaks not only depend on egg mass abundance, but also on dead moths or their larval and pupal skins which then are numerous on cork oaks. The 1986–1990 gypsy moth outbreak occurred in the part of the Mamora forest where tree damage by man and xylophagous insects were common. Unhealthy cork oaks, by providing abundant shelter for numerous arthropods are beneficial to the oophagous predators which find various and abundant food sources there. In this way, forest degradation probably explains why egg predator activity in the infested area rapidly increased so that the pest outbreak collapsed (Villemant & Ramzi, 1995).

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