

Zeitschrift: Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society

Herausgeber: Schweizerische Entomologische Gesellschaft

Band: 48 (1975)

Heft: 1-2: Fascicule-jubilé pour le 70e anniversaire du Prof. Dr. Paul Bovey = Festschrift zum 70. Geburtstag von Prof. Dr. Paul Bovey

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DOI: <https://doi.org/10.5169/seals-401753>

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The regulating action of egg predators on the populations of *Zeiraphera diniana* Guénée (Lep. Tortricidae)¹

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The eggs of the grey larch tortrix *Zeiraphera diniana* GUÉNÉE are partially destroyed by *Acarina* and probably by *Dermaptera* at Zuoz and Madulain, Upper Engadine Valley, and by *Heteroptera* and *Neuroptera* at Lenzburg, near Zürich. The predation could be evaluated by exposing larch sticks with *Z. diniana* eggs on branches of larch trees. The total predation on the exposed sticks varied from about 30% (Madulain) to nearly 85% (Lenzburg) during the summer and was rather constant over 3 consecutive years in each locality, irrespective of the natural density of the host eggs. The predation activity during the summer decreased, however, with decreasing egg density.

Action régulatrice des prédateurs oophages sur les populations de Z. diniana.

Les œufs de la tordeuse grise du mélèze, *Zeiraphera diniana* GUÉNÉE, sont la proie d'Acariens et peut-être de Dermaptères dans les localités de Zuoz et Madulain, Haute-Engadine, et d'Hétéroptères et de Neuroptères à Lenzburg, près de Zurich. La prédation a été évaluée en exposant sur les branches de mélèze des tronçons de branchettes avec des pontes de tordeuse. La prédation totale des œufs sur ces tronçons de branchettes a varié entre environ 30% (Madulain) et 85% (Lenzburg) pendant l'été et est demeurée assez constante d'une année à l'autre dans chacune des localités, indépendamment de la densité des œufs des populations naturelles de *Z. diniana*. On a pu constater que l'activité de prédation diminue au cours de l'été parallèlement à la diminution de la densité des œufs.

1. INTRODUCTION

The grey larch tortrix, *Zeiraphera diniana* GUÉNÉE (Lep. Tortricidae), is a univoltine species. The longest developmental period in the ontogenesis of the insect is the egg stage. Eggs are deposited during the summer, beginning in June in the lowlands and in August in the highest parts of its area of distribution. They have an obligate diapause (BASSAND, 1965) and hatch in April to June of the following year according to altitude. In Europe the optimum zone of development of *Z. diniana* ranges from 1600 to 2000 m a. s. l. In this zone there is a well marked cyclic variation in abundance with a 20 000 fold population increase in 4 to 5 generations and the appearance of visible damage (defoliation) during 2 to 3 years of maximum population density (BALTENSWEILER, 1968). The amplitude of the fluctuations decreases with the altitude. The populations of *Z. diniana* are almost stable at a low density on the Swiss Plateau (500 to 600 m a. s. l.).

Eggs of *Z. diniana* are naturally parasitized by a species of *Trichogramma* (Hym. Chalcidoidea), but the degree of parasitism is usually very low. Between 1970 and 1972 it varied between 0.6 and 3.8%. Because of the long egg stage of

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the host and the existing mass rearing techniques for *Trichogramma*, the parasitoid was selected for utilization in mass release operations. In 1969 preliminary studies on the dispersal of the parasitoid were initiated in the Upper Engadine Valley. It appeared, however, that many exposed eggs were destroyed by predators during the summer months and that the action of the parasitoid might be nullified by the interference of predators. The role of predators in limiting *Z. diniana* populations in the egg stage was therefore studied during the three subsequent years, 1970–1972, in three localities – Zuoz and Madulain, 1800 m a. s. l., in the Upper Engadine Valley, and Lenzburg, 550 m a. s. l., about 30 km west of Zürich. In the experimental area at Zuoz visible damage occurs at every gradation of *Z. diniana*, in that of Madulain visible damage does not occur or is very limited (Dr. C. Auer, *pers. comm.*).



Fig. 1: Distribution of the sticks with eggs of *Z. diniana* on a larch branch.

2. METHODS

2.1 Detection of predators of *Z. diniana* eggs

Last instar larvae of *Z. diniana* were tagged with a radioactive marker (less than 1 μ c of Zn^{65} per larva) injected in the general body cavity through an abdominal leg. The resulting tagged moths oviposited in the laboratory, the technique for egg production described by MEYER (1969) and ALTWEGG (1971) being used. However, instead of cardboard strips for oviposition, larch sticks were used of 5 (Lenzburg) and 10 (Zuoz and Madulain) cm length and 6 to 10 mm in diameter, the sticks being naturally covered with lichens. The sticks, which were tapered at one end, were held for 24 hours at 80 °C to kill any

arthropods. Five sticks were exposed to 10 tagged females of *Z. diniana* for 12 hours and the mean number of tagged eggs deposited per stick was 9.3 (based on counts for 20% of the sticks). The sticks were then fixed to larch branches in the experimental areas in the forest by inserting the tapered ends into corresponding holes drilled in the branches. Five or six sticks were fixed to a branch (fig. 1) which was then enclosed by a large muslin (organdy) sack (fig. 2). After two weeks the enclosed branches were cut off, and the arthropods collected with a



Fig. 2: Larch branch with sticks enclosed in a muslin sack.

BERLESE-TULLGREN funnel and examined. Scintillation detection of the collected arthropods was made at the end of the season. Six branches (one per tree; each tree 20 to 30 m high) oriented north and south and about 3 m above the ground were examined for each of the 3 years of experimentation at Zuoz.

In Lenzburg, the sticks with tagged eggs were not enclosed. Branches with egg sticks were beaten and the falling arthropods collected in a net. Scintillation detection of arthropods was made as above.

2.2 Evaluation of predation of *Z. diniana* eggs

Untagged moths were used for oviposition on larch sticks in captivity. The egg density per stick, based on counts for 20% of the sticks used, varied from 5 to 65.5; for the material used in Zuoz and Madulain during 3 years the average density was 19.8 eggs per stick, and for Lenzburg it was 26 eggs per stick. Considering the summer period only, when predator activity is most intense, sticks used had an egg density of 24.8 in 1970, 13.2 in 1971, and 13.3 in 1972. Sticks were inserted into holes made in the branches as shown in fig. 1, using branches with

north and south orientation and at different levels above ground (up to 12 m). According to altitude, they were exposed to predators for 2 to 5 weeks in summer, 5 to 6 months in autumn and winter, and 5 to 6 weeks at the beginning of the spring (tables 2 and 3). In 1970 the sticks were replaced after each period of exposure and only one series of sticks was exposed during the whole developmental period of the eggs. In 1971 and 1972 the duration of exposure was modified in Zuoz and Madulain, the sticks being exposed altogether from the beginning of the oviposition of *Z. diniana* in nature; a quarter of the sticks present were collected every two weeks and predation evaluated until October only, the impact of predators from October to April being negligible (table 3). Sticks were preserved at 2 °C after exposure and collection.

Altogether nearly 1600 sticks were prepared and 80% of them, with about 28 000 eggs, were exposed; 1.5% of the sticks were lost because of inadequate fixation, and 1.1% of the eggs were damaged during manipulation.

Experiments started at the end of June in Lenzburg, and in Zuoz and Madulain at mid August, when the oviposition of *Z. diniana* had already started in nature.

Table 1: Arthropods obtained from branches of larch trees enclosed by a muslin sack between 12 August and 30 September 1972 using the technique described under 2.1. Locality: Zuoz, 1800 m a. s. l.

Arthropods collected in muslin sacks	Number of individuals obtained from 6 branches		
	from 12.8 to 26.8	from 26.8 to 9.9	from 9.9 to 30.9
Collembola	2,064	2,730	2,534
Dermaptera	6 ^a	20 ^a	5 ^a
Psocoptera	170	24	40
Heteroptera	2	0	0
Auchenorrhyncha	12	6	7
Other Insects & Myriapoda	40	9	9
Aranida	8	6	10
Acarina Mesostigmata	21	2	0
Bdellidae & Anystiidae	26	24 ^a	23
Erythraeidae	115 ^a	94 ^a	36 ^a
Oribatidae	1,242	103	207

^a = tagged with radioactive tracer

3. RESULTS

3.1 The complex of species preying upon *Z. diniana* eggs

In Zuoz only representatives of *Dermaptera* and of *Acarina* were detected as predators of *Z. diniana* eggs (table 1). The species of *Dermaptera* were ignored; their behaviour suggested that they preyed upon tagged predaceous mites rather than upon tagged eggs of *Z. diniana*. The *Acarina* were represented by the genera *Balaustium* (*Erythraeidae*) and *Bdella* (*Bdellidae*). The most frequent species of

Balaustium was *B. murorum* HERRMANN⁴, which is common in the Alps up to 2600 m a. s. l. (SCHWEIZER & BADER, 1963). All individuals tagged with radioactive tracer were in the adult stage. The genus *Bdella* was represented by *B. vulgaris* HERRMANN⁴, which seemed to be mainly confined to the litter. Predation by the mites was often observed in nature. The relative importance of *B. murorum*, *B. vulgaris* and of the *Dermaptera*, based on the number of the tagged individuals, was 71:9:20.

In Lenzburg the most important predator of *Z. diniana* eggs was the mirid *Deraeocoris annulipes* HERRICH-SCHÄFFER⁵, which was very common during spring and summer (GRAF, 1973). Unidentified *Neuroptera* larvae were also detected preying on *Z. diniana* eggs, but their number, compared with that of the mirids, was very small.

Table 2: Predation of *Z. diniana* eggs during 5 subsequent periods of egg development. Average number of eggs per stick = 19.8 (Zuoz and Madulain) and 26 (Lenzburg)

Periods ^a	Average predation in % of eggs exposed					
	Zuoz		Madulain		Lenzburg	
	observed	calculated (cumulative)	observed	calculated (cumulative)	observed	calculated (cumulative)
1	28	28	21,7	21,7	52,7	52,7
2	26,9	47,4 ^b	18,7	36,3	54	78
3	23	59,5 ^b	16,8	47	30,5	84,7
4	7,8	62,6	10,7	52,7	9,6	86,2
5	6	64,9	6,4	55,7	7,6	87,2

^a = 15.8-1.9/ 1.9-17.9/ 17.9-30.10/ 30.10.1970-22.4.1971/ 22.4-25.5 for Zuoz and Madulain

22.6-22.7/ 22.7-25.8/ 25.8-29.9/ 29.9.1971-6.3.1972/ 6.3-16.4 for Lenzburg

^b = 26,9% of (100-28) + 28; 23% of (100-47,4) + 47,4; etc.

3.2 The importance of predation of *Z. diniana* eggs

Most of the *Z. diniana* eggs on sticks were destroyed by predators during the summer (table 2). In Zuoz and Madulain as well as in Lenzburg predation much decreased from October onwards and remained low during the spring prior to egg hatch. Egg predation in Madulain was generally lower than in Zuoz, but only the difference for the 2nd period is statistically significant ($P = 0.05$). Predation in Lenzburg was higher than in Zuoz or Madulain, probably because the egg stage is longer in summer. In Zuoz, total predation calculated on the basis of 5 consecutive periods of exposure was 64.9% (table 2). This is higher than the predation on sticks exposed continuously during the whole period, i. e. 15 August to 25 May, which was 47.6%. This indicates that predation is high if a high egg density is maintained (19.8 eggs/stick every 2 weeks) and that predation decreases with decreasing egg density (the same sticks exposed from 15 August to 25 May).

⁴ det. Dr. C. Bader, Nat. Hist. Museum, Basel

⁵ det. Dr. R. H. Cobben, Laboratory of Entomology, Fac. of Agriculture, Wageningen

Because of the reduced activity of predators during fall and winter, experiments were conducted in 1971 and 1972 until October only. The results were compared with those obtained for the same period in previous years. They are all summarized in table 3. It appears that the rate of predation remains rather

Table 3: Predation of *Z. diniana* eggs during the summer (July–October) in different years (1970–1972) and in different localities.

Periods ^a	Average predation in % of eggs exposed							
	Zuoz 1970 ^b	Madulain 1970 ^b	Zuoz 1971 ^c	Madulain 1971 ^c	Zuoz 1972 ^c	Madulain 1972 ^c	Lenzburg 1970 ^c	Lenzburg 1971 ^b
1	28	21,7	28,4	23,5	33,1	21,2	–	52,7
2	47,4	36,3	39,7	18,3	35,7	33,1	–	78,1
3	59,5	47	42,6	22,7	38	38	–	84,7
4	–	–	51,5	30,7	50,9	37,8	61,5	–

^a = 15.8–1.9/ 1.9–17.9/ 17.9–30.10 for Zuoz and Madulain in 1970
 12.8–26.8/ 12.8–9.9/ 12.8–30.9/ 12.8–15.10 for Zuoz and Madulain in 1971
 14.8–28.8/ 14.8–12.9/ 14.8–28.9/ 14.8–18.10 for Zuoz and Madulain in 1972
 27.7–2.11 for Lenzburg in 1970
 22.6–22.7/ 22.7–25.8/ 25.8–29.9 for Lenzburg in 1971

^b = calculated (cumulative)

^c = observed (cumulative)

Table 4: Predation of *Z. diniana* eggs on branches with different orientation and at different levels above ground. Locality: Zuoz, 1800 m a. s. l.

Periods ^a	Observed average predation in % of eggs exposed			
	south 2 m level	north 2 m level	south 12 m level	north 12 m level
1	30,4	12,4	25,4	12,9
2	31,8	37,7	23,4	20,8
3	21	18,3	27,1	15,9
4	5,6	17,7	8,8	3,4
5	12,5	7,7	0	19

^a = 15.8–1.9/ 1.9–17.9/ 17.9–30.10/ 30.10.1970–22.4.1971/
 22.4–25.5.1971

constant over the years for the same locality. The predation during a season seems to increase more regularly in Zuoz than in Madulain, but the difference between the two localities is significant ($P = 0.001$) for 1971 only.

Predation was evaluated for different orientations of the branches with respect to the trunk and for different levels above ground (table 4). In general predators seem more active on branches oriented to the south. The differences between the two levels of 2 and 12 m above ground of the south orientation are

not significant. On the contrary, the differences between the two levels of the north orientation are highly significant ($P = 0.001$) for the periods 1.9–17.9 and 30.10–22.4. On the north oriented branches predators appear to be more active on branches near the ground.

In the Upper Engadine Valley eggs are laid by *Z. diniana* under the lichens which usually grow on the distal portion of branches up to 20 mm thick. It was shown in two subsequent years that the activity of predators is greater on the distal part of the branches than on the proximal portion (table 5). Except for the period 5 in 1970/71 and the period 4 in 1971, the differences between the two positions are significant.

Table 5: Predation of *Z. diniana* eggs on different portions of branches of larch trees in Zuoz, 1800 m a. s. l.

Periods ^a	Observed average predation in % of eggs exposed			
	1970/71		1971	
	proximal portion	distal portion	proximal portion	distal portion
1	18,3	32,3	24,4	35,4
2	7,3	46,7	31,6	47,8
3	13,2	42,7	37,7	47
4	0	9,6	58	53
5	25	13,8	–	–

^a= 15.8–1.9/ 1.9–17.9/ 17.9–30.10/ 30.10.1970–22.4.1971/
22.4–25.5 for 1970–71.

12.8–26.8/ 26.8–9.9/ 9.9–30.9/ 30.9–15.10 for 1971.

4. DISCUSSION

The interpretation of the results obtained is not easy, as many elements of the predator-prey relationship remain unknown. Egg predation remained rather similar over the years. In fact, the calculated cumulative predation in Zuoz (1800 m a. s. l.) was 59.1% of the exposed eggs in 1969 and 59.5% in 1970; the observed cumulative predation was 51.5% in 1971 and 50.9% in 1972. Considering the whole egg stage (summer to spring of the following year), these values should be a little higher. In Lenzburg (550 m a. s. l.) the predators destroyed during the whole egg stage 69.4% of the exposed eggs in 1969–70, 81.9% in 1970–71, and 87.2% in 1971–72, with an average of 79.5% for the 3-year period. The higher figures obtained in Lenzburg may be due to the longer period of exposure (the egg stage being longer than in Zuoz during summer, at least for a part of the population), to the different behaviour of the predators (which belong to different orders than those at Zuoz), and to the higher egg density of the sticks (see methods).

The experiments were carried out during the progression phase of a gradation of *Z. diniana*. The moth population density in Zuoz, for instance, evaluated at the 3rd–4th larval stages, was 0.34/kg twigs in 1969, 2.56/kg in 1970, 15.22/kg in 1971, and 196/kg in 1972 (AUER, 1973). The corresponding egg densities are unknown. Assuming a mortality of 80% during the egg and first 3 larval stages (predation, parasitism, lack of coincidence, etc.), the initial egg density for each of the 4 years considered is estimated at 1.7, 12.8, 76.1 and 980. As one branch from the trunk has roughly 1 kg twigs, equivalent to 50 m length the above values represent the egg number per branch. Considering the branch as a unit on which predators move, an average of 100 eggs were added by placing 5 or 6 sticks on a branch. The increased number might have a certain significance in 1969, when the natural egg density was low, but was of little importance in 1972, when the natural egg density was high. At least in 1972 it can be assumed that predation on the branches was as high as on the sticks and was therefore an important mortality factor.

Table 6: Variation of *B. murorum* density per dm³ larch branches in two different years on different portions of the branches. Locality: Zuoz, 1800 m a. s. l. (each value = mean of 8 samples).

Sampling date in 1971	Portion of the branch		Sampling date in 1972	Portion of the branch	
	proximal	distal		proximal	distal
-	-	-	14.8	24	26,8
26.8	9,7	28,7	28.8	10,5	16,8
10.9	17,3	14	12.9	6,8	19,8
30.9	1,3	6,7	-	-	-

The interpretation is different if the egg density on the branches is correlated with the egg density on the sticks. The surface of a branch where oviposition occurred was very variable, with an average of 11 000 cm²; the mean surface of a stick was 24 cm². The sticks exposed during the summer 1972 had an average of 13 eggs (see 2.2). In the same year there were 980 eggs (estimated) for 11 000 cm², i. e., 1 egg for about 11 cm² or about 2 eggs for a surface corresponding to that of a stick. Therefore, in 1972 the egg density of a stick was 6 to 7 times that of the natural population. Under these conditions it is difficult to say whether the results obtained can be extrapolated, as the behaviour of the predators and the natural distribution of the eggs on the branch are unknown. In general, predation on the sticks was high at high egg density (table 2) and decreased when density decreased (table 3). As the main predaceous species does not show a change in density from one year to the other (table 6), the functional response of the predators seems to follow the progression trend of the *Z. diniana* population.

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