

The parasitoid complex of *Epinotia tedella* (Cl.) (Lepidoptera: Tortricidae)

MIKAEL MÜNSTER-SWENDSEN

Münster-Swendsen, M.: The parasitoid complex of *Epinotia tedella* (Cl.) (Lepidoptera: Tortricidae).

Ent. Meddr, 47: 63–71. Copenhagen, Denmark 1979. ISSN 0013–8851.

The parasitoid species attacking *Epinotia tedella* (Cl.) in North Zealand, Denmark, have been studied during nine years. *Pimplopterus dubius* (Hgn.) and *Apanteles tedellae* Nix. were the dominant primary parasitoids. *Campoplex cursitans* (Hgn.) and *Exochus tibialis* Hgn. were both cleptoparasitoids associated with *A. tedellae* and *P. dubius*, respectively, whereas *Mesochorus silvarum* Curt. was the only hyperparasitoid, which attacked all of the above mentioned parasitoids. Summarized data on phenology and biology of the species are presented in the paper. *P. dubius* and *A. tedellae* cannot discriminate between parasitized/unparasitized hosts, leading to random super- and multiparasitism, but the distributions in time and space of their attacks are not identical. Means and ranges of parasitism found in different stands and years are presented, as well as a general scheme on the outcome of the multiparasitic competition.

Mikael Münster-Swendsen, Institut for almen Zoologi, Universitetsparken 15, DK–2100 København Ø, Danmark.

Introduction

The spruce needleminer, *Epinotia tedella* (Cl.), is a well known pest insect on Norway Spruce (*Picea abies* Karst.) throughout Europe.

Over a period of nine years (1970–1978), the population dynamics of *E. tedella* has been studied in a stand of Norway Spruce (treeage: 34 years in 1978) in the forest Gribskov, North Zealand in Denmark. During the study it became apparent that parasitoids significantly affect the population dynamics of *E. tedella*.

The present paper summarizes the data on phenology and relative importance of the individual parasitoid species and their associated clepto- and hyperparasitoids, and describes the interspecific relations and the competitive aspects related to multiparasitism.

Host biology and collecting of data

E. tedella emerges from the forest floor in June. The female deposits her eggs singly on the needles in the canopy, where the first larval instar appears in July. The larva mines in the needles until November, when it spins down from the canopy to hibernate in a cocoon in the

forest floor. Pupation takes place in May and the pupal period lasts 3–4 weeks.

In mid-August, host larvae were collected from branch samples and dissected in the laboratory. At this time of the year all parasitoid attacks on *E. tedella* had occurred and it was then possible to detect the degree of superparasitism, multiparasitism and encapsulation and to trace the outcome of any kind of competition among the parasitoid larvae (Münster-Swendsen, 1973a), though the host larva was only about 2 mm long and had to be dissected with fine insect-pins.

When the host larvae spun down from the canopy in November and December, they were sampled in 200 funnel traps. These were attended every week and the larvae caught were immediately counted and dissected.

In May, host and parasitoid mortalities were assessed from host cocoons sampled from the forest floor.

In June and July, 200 emergence traps of a type described by Münster-Swendsen (1973b) were placed on the forest floor for sampling of the emerging host and parasitoid populations.

The trap glasses were attended every week and hosts and parasitoids were identified, counted and sexed.

The abundance of hosts and parasitoids in different spruce stands was studied by taking branch samples from stands of varying ages in 8 different forests in North Zealand in 1971, and by the use of trap funnels in different stands in Gribskov forest in 1977 and 1978.

Parasitoid species

In North Zealand the following parasitoid species were found on *E. tedella* through investigations of about 10,000 host individuals:

Hymenoptera Ichneumonidae:

- Pimplouterus (Lissonota) dubius* (Hgn.)
- Mesochorus silvarum* Curt.
- Campoplex cursitans* (Hgn.)
- Exochus tibialis* Hgn.

Braconidae:

- Apanteles tedellae* Nix.
- Agathis? cingulipes* Nees.

Tetracampidae:

- Dipriocampe* sp.

Trichogrammatidae:

- Trichogramma evanescens* Westw.

Diptera Tachinidae:

- Unidentified larvae.

Parasitoids known, or assumed to be associated with *E. tedella* in Austria and Germany have earlier been recorded (Schedl, 1951; Führer, 1964), but in most cases the findings were based on the use of emergence-traps and -boxes, a method that often leaves a great deal of uncertainty with respect to the true host species of the collected parasitoid and gives no information on the relationships between the parasitoid species. Further, these investigations were carried out during outbreaks of *E. tedella*, whereby unusual parasitoid abundance might have appeared. The species composition found by Führer (1964) in Schleswig-Holstein is very close to that found in the present investigation.

Epinotia nanana Tr. and *Pseudohermenias claus-thaliana* (Sax.) both live on Norway Spruce and have a biology similar to that of *E. tedella*, but they were both less abundant than *E. tedella*, which was the predominant lepidopteran species in all stands. The parasitoids of the former two species were studied in order to observe

whether any of the larval endo-parasitoids of *E. tedella* could be found. No such overlap was observed except for one incident, where a larva identical with that of *A.? cingulipes* was found in *E. nanana*, whereas an *Agathis*-species frequently found in *P. claus-thaliana* was surely not identical with that in *E. tedella*.

Thus, at least *P. dubius* and *A. tedellae* can be regarded as strongly host-specific in a pure spruce stand. *A. tedellae* is described as genuinely host-specific by Capek (1969), whereas *P. dubius*, though well adapted to *E. tedella*, has been recorded from other host species, according to Thompson (1957). This might be due to confusion concerning the identification and taxonomy of the parasitoids (Capek, 1969).

All the Ichneumonidae and Braconidae found on *E. tedella* are monovoltine and solitary endo-parasitoids, attacking the host in its first or second larval instar. Parasitoids attacking the pupal stage have neither been found in the present study nor in other studies on *E. tedella*.

1. *Pimplouterus dubius* (Hgn.)

The species is a primary parasitoid attacking the first larval instar (L₁) of *E. tedella* from late June till the end of July. The adults emerge between 10 June and 15 July with a protandry of about 10 days. The sex-ratio of different generations varies and ♀/♂-ratios between 0.66 and 2.73 (mean and S. E.: 1.67 ± 0.27) have been observed during eight years within a single spruce stand. The individual female probably spends some days swarming and mating before searching and oviposition is commenced. She follows a particular behavioural sequence during the detection and parasitism of the host: When the female finds the small pile of faecal pellets fixed by the host larva outside the entrance to the mine, she investigates the pile closely by intense palpations by the antennae. She then liberates the fine, 6 mm long ovipositor from the valvae, leads it through the entrance of the mine, moves a little to let the ovipositor follow the mine, and remains quiet for a moment, apparently depositing the egg. After withdrawal of the ovipositor, she cleans it with her hind legs and brings it in position between the valvae again. This sequence is followed by intense cleaning of the whole body and especially of the antennae. The total »handling time« (Holling, 1959) lasted between 40 and 120 seconds in the

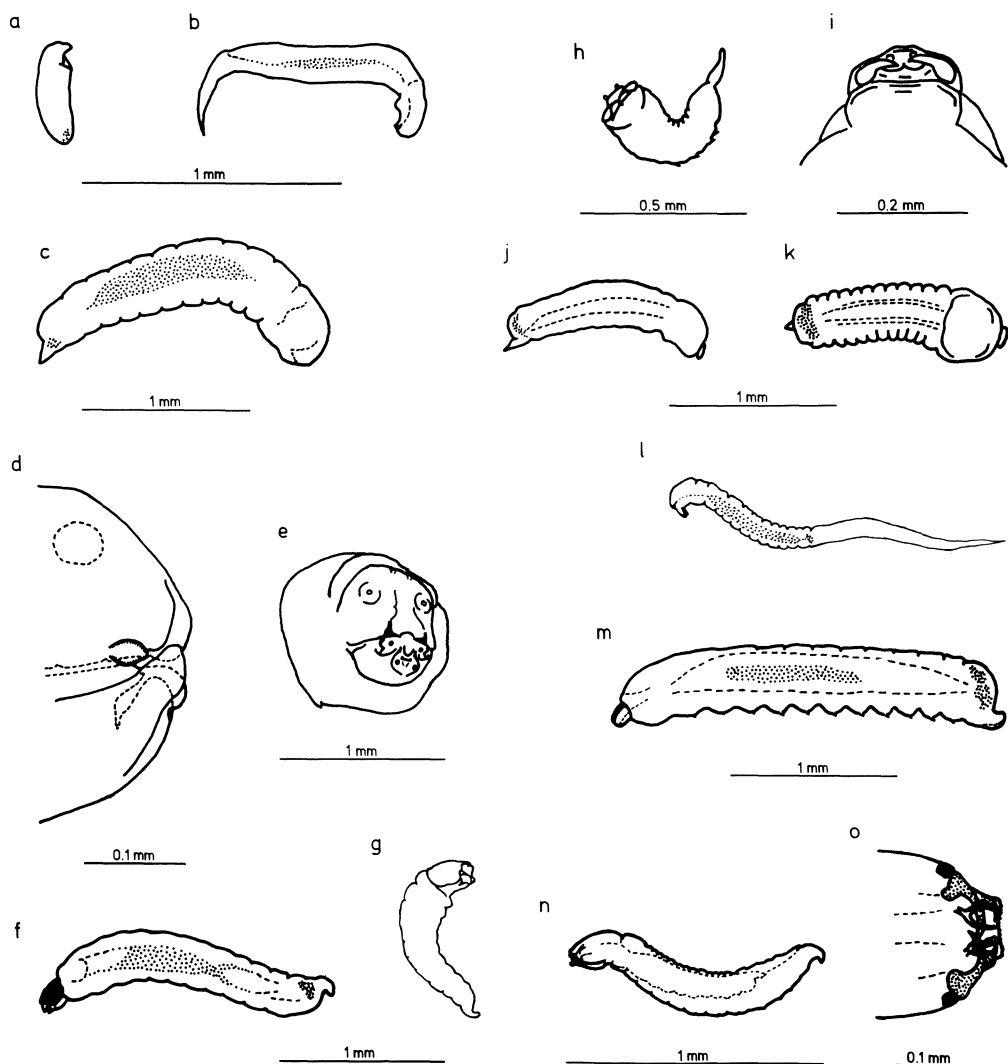


Fig. 1. Egg and larvae of larval endoparasitoids from *E. tedella*. *P. dubius* (a-e), eggchorion (a), early L₁ (b), L₂ (c), head of L₂ (d) and head of L₅ (e). *E. tibialis* (f-g), late L₁ (f) and early L₁ (g). *A. tedellae* (h-k), early L₁ (h), head of L₁, ventral view (i), late L₁, lateral view (j) and dorsal view (k). *C. cursitans*, L₁ (l). *A.? cingulipes*, late L₁ (m). *M. silvarum* (n-o), early L₁ lateral view (n) and head, ventral view (o).

laboratory, where all these observations took place.

A host larva placed outside a mine was not noticed by the searching parasitoid and never released an oviposition behaviour; in addition, it was observed that host larvae in mines longer than 6 mm could not be reached by *P. dubius*. To produce a 6–7 mm long mine only takes the newly emerged larva 3–5 days after which it is

protected against attacks. This short-time susceptibility of the host results in synchronization aspects of importance in the dynamics of the species (Münster-Swendsen & Nachman, 1978).

The egg is deposited in the haemolymph of the host and can be found in various places within the host body during the next 5 days. The newly hatched parasitoid larva is mainly found in the anterior part of the host, whereas the

older larva is found in the posterior part (Jørgensen, 1975). According to Jørgensen, these changing positions play a role in the intra- and interspecific competition between parasitoid larvae.

P. dubius has five larval instars some of which are shown in Fig. 1 b-e. The first ecdysis takes place about 1 October and often coincides with an ecdysis of the host. *P. dubius* hibernates as L_2 within the host in the forest floor, and not until ultimo April does it continue its development and eats the host larva. L_3 leaves the fragile integument of the dead host, and, within the host cocoon, it spins a light cocoon, which darkens at the rear end due to ejection of the larval meconium. The pupal stage lasts about one month.

The female of *P. dubius* is not capable of avoiding already parasitized hosts and superparasitism followed by intraspecific competition among the larvae is frequently found. In the case of superparasitism only one parasitoid larva, usually the oldest and biggest, survives while the other larvae in the host are suppressed physiologically and sooner or later die. This suppression is often followed by encapsulation by haemocytes of the host.

The degree of superparasitism has been measured on several occasions, and in all cases

the results fit a Poisson-series (Fig. 2a), corresponding to an apparent random search for hosts, combined with complete absence of discrimination ability. However, a Poisson-series could have appeared if search was not random, or, for other reasons, all hosts did not have the same chance of being found and attacked, and if a certain degree of discrimination was present.

Generally, the defence mechanism of the host is ineffective against the well adapted *P. dubius*, but a few parasitoid larvae are nevertheless encapsulated by haemocytes. Thus, out of 317 single eggs or larvae 10 eggs and 4 larvae were encapsulated.

The presence of the small *P. dubius* larva provokes some changes in the host, as the development of gonads and wing buds are suppressed (Führer, 1972, 1973); further, the time at which the host leaves the canopy is delayed.

2. *Apanteles tedellae* Nix.

This primary parasitoid attacked L_1 and L_2 from the beginning of July till the beginning of August. The adults emerged between 15 June and 15 July with a protandry of about 9 days. ♀/♂-ratios between 0.72 and 1.23 (mean and S. E.: 1.06 ± 0.12) were observed in a single stand. For both *A. tedellae* and *P. dubius* male domi-

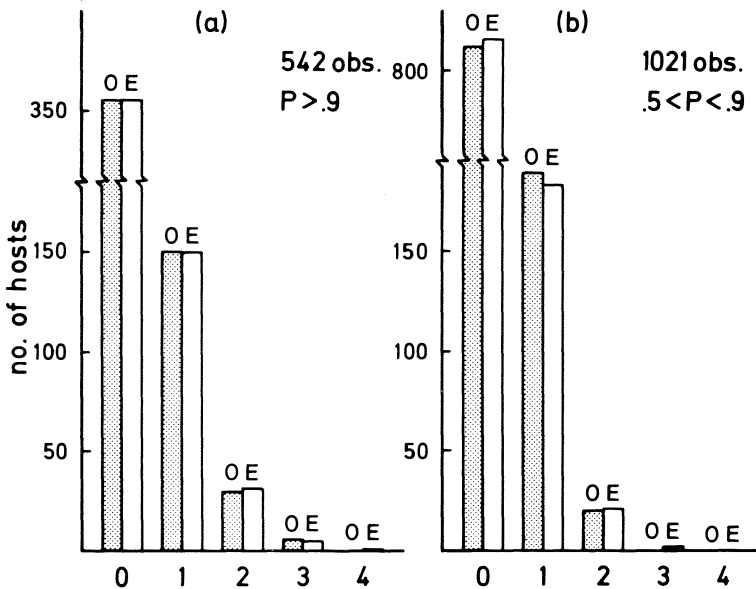


Fig. 2. Observed (O) and expected (E) numbers of *E. tedella* containing 0-4 parasitoids in their body. The expected numbers refer to a Poisson-series. *P. dubius* (a), and *A. tedellae* (b).

nance was only observed in one year (1975), while the other years showed an excess of females. Little is known about the behaviour of the adult *A. tedellae*, except that the female may oviposit in the host larva simply by penetrating the mine wall with her 1 mm long ovipositor. This behaviour creates no synchronization problems.

The egg and larva (Fig. 1h-k) are found in the haemolymph within the abdomen of the host. Three larval stages exist and *A. tedellae* hibernates as L₁ within the host. After leaving the dead host in May, L₃ spins a cocoon and pupates within the host cocoon. The cocoon of *A. tedellae* is a little shorter than that of *P. dubius*, and is covered by a few light-brown threads.

A. tedellae is not capable of avoiding superparasitism, and the first larva to arrive will attack another egg or larva of its own species, and of other species. It bites the competitor, keeping the mandibles in its body for some time, a situation often found during the dissections. Finally, the damaged larva is killed by encapsulation of host haemocytes.

The spatial distribution of attacks on hosts was found to be contagious, and hence, a random distribution of eggs and larvae among hosts, i. e. a Poisson-series, would not appear if discrimination between parasitized/unparasitized hosts was totally absent. Samples from branch sections at one particular canopy-height showed a distribution that followed a Poisson-series (Fig. 2b) when sampling was performed with a view to eliminate the effect of spatial distribution. The results may thus be interpreted as a local random search on branches. In other words, the search in great scale is aggregated, but the species has no capability of discrimination.

No solitary *A. tedellae* larva has ever been found encapsulated within the host, emphasizing the good adaptation to the host species. The effect on the host is also more pronounced than that of *P. dubius*. In addition to the suppression of gonads and wing buds, larval colours do not develop and the size and weight of the host decrease appreciably (Führer, 1970, 1972, 1973).

3. *Mesochorus silvarum* Curt.

M. silvarum was found being a hyperparasitoid in larvae of both *P. dubius*, *A. tedellae*, *C. cursitans*, *E. tibialis* and *A.? cingulipes*. The adults emerged during the period 15 June – 15 July

with a protandry of about one week. The ♀/♂-ratio varied between 0.44 and 0.67. The egg is deposited in the haemolymph of the parasitoid larva located within *E. tedella*, and is found at different places within the body. The number of larval stages is not known, but *M. silvarum* hibernates as a small L₁ (Fig. 1 n-o) within the still living parasitoid.

Superparasitism occurs and up to three larvae have been found in a single *P. dubius* larva. In that case only one was alive while the others had been suppressed or directly killed and appeared small and sleazy. An egg of *M. silvarum* was once found free in the haemolymph of an *E. tedella* which did not contain any other parasitoid, but the egg had not hatched, though it was found on 10 November. On a few occasions solitary eggs of *M. silvarum* have been found encapsulated by haemocytes and thus destroyed in both *P. dubius* and *A. tedellae*.

Hyperparasitism of the rather transparent L₁ of *A. tedellae* can be detected directly under suitable light conditions in the microscope, whereas the larvae of *P. dubius* have to be dissected to ascertain whether they are hyperparasitized; the parasitized parasitoid larva is often smaller and has a “humpback-like” appearance and is apparently somewhat weakened, as the lepidopteran host is less affected by its presence than usual.

4. *Campoplex cursitans* (Hgn.)

Close investigations through all years have shown that *C. cursitans* is an obligate cleptoparasitoid, as it does not attack unparasitized larvae of *E. tedella*, but only those that have been parasitized specifically by *A. tedellae*. However, on very few occasions, it has been found together with *A.? cingulipes*, *P. dubius* and *E. tibialis*. The adults emerged during the period 20 June – 25 July, with a protandry of about 8 days, and ♀/♂-ratios between .64 and .87.

The first instar larva (Fig. 11) is found in the haemolymph in the thoracic region of the larva of *E. tedella*. *C. cursitans* hibernates as L₁ and completes its development during May and June at the expense of the host. L₁ has only rudimentary mandibles and suppresses its competitors physiologically, but the typical anterior position in the host seems to be necessary for successful suppression. Thus *A. tedellae* (and other competitors) inevitably dies if *C. cursitans* occupies

its anterior residence, but on nine occasions, where it was found in the abdomen of the host, both parasitoids were still alive in December though they were a little smaller than usual. Functionally *C. cursitans* can be compared with a hyperparasitoid as it is the primary enemy of another parasitoid species, and only attacks larvae of *E. tedella* that are bound to die.

When *C. cursitans* itself is hyperparasitized by *M. silvarum* the effect on *A. tedellae* is either the usual suppression or a situation where *A. tedellae* is alive and normal while *C. cursitans* is small and weak. Neither superparasitism nor encapsulation by haemocytes have been observed.

The effect on the host is difficult to observe as the presence of the young larva of *A. tedellae* has already induced the changes, mentioned above, prior to its early death. Yet, these changes are less pronounced when *C. cursitans* is present. (At 1 November the mean fresh-weights of host larvae (L_3) that were unparasitized, and parasitized by *P. dubius*, *A. tedellae* and (*C. cursitans* + *A. tedellae*) were 6.17, 5.90, 3.99 and 4.82 mg, respectively).

It is not known how closely *C. cursitans* is connected with *E. tedella*, but investigations of a large number of larvae of *P. clausthaliana* and *E. nanana* did not yield this species. The connection with *A. tedellae* might be interpreted as a specific connection with *E. tedella* as well, but *C. cursitans* might well be associated with other braconid species attacking other host species.

5. *Exochus tibialis* Hgn.

E. tibialis attacks the first and second instars of *E. tedella* larvae and has been observed in host larvae from 10 July. The adults emerged from 23 June till 9 July with 4–5 days protandry. L_1 (Fig. 1f-g) was found in the haemolymph in the abdomen of the host throughout the autumn and winter, and, without exception, together with dead or dying larvae of *P. dubius*. Thus, *E. tibialis* must be considered a cleptoparasitoid attracted to hosts that are parasitized by *P. dubius*. This may explain why Führer (1964) found the species especially in young stands where *P. dubius* is also the dominant parasitoid.

Superparasitism does occur and up to four *E. tibialis* larvae have been found together with one *P. dubius* larva in a single host. In the case of superparasitism only one larva survives, just as *E. tibialis* always kills a *P. dubius* larva, probably by means of its mandibles.

6. *Agathis? cingulipes* Nees

A? cingulipes is a primary parasitoid attacking L_1 or L_2 of *E. tedella* during the first two weeks of July, and the species hibernates as L_1 (Fig. 1m) in the host larva. The larvae are found at different places within the host, though mainly in the abdomen. Super- and multiparasitism occur and *A.? cingulipes* probably uses its well developed mandibles in the competitive combat.

The influence on the host physiology is much less pronounced than that of the other primary parasitoids. The reason might be that *A.? cingulipes* is primarily adapted to another host species, e. g. *E. nanana*.

7. *Trichogramma evanescens* Westw.

T. evanescens is a well known egg-parasitoid found on several Lepidoptera-species, and its development in eggs of *E. tedella* has been described by Schedl (1951).

The highest percentage parasitism found during the long-term investigation in Denmark was 32.8 (in 1973) while other years showed percentages between 6.9 and 16.7. No significant response to host aggregations has been found; neither was there any demonstrable correlation between the degree of parasitism and the position of eggs on needles or branches.

8. *Dipriocampe* sp.

The species was found as an ectoparasitoid on L_3 and L_4 of *E. tedella*; it was also found on *P. clausthaliana* in October. In October the larva pupates inside the mine of *E. tedella*, without making a cocoon. The adults emerge the following spring and must then attack other host-species.

Führer (1970) has found *Euderus albitarsis* Zett. (Hymenoptera: Eulophidae) as an ectoparasitoid on *E. tedella*, but this species was never found in the present investigation. *Dipriocampe* sp. only occurred in certain years and never exceeded 0.2 per cent parasitism. Consequently, it must be regarded as insignificant in the dynamics of *E. tedella*.

Frequency and interrelations

When data from all years and stands were used, the means and ranges of larval parasitism shown in Table I were found.

In general, *P. dubius* was the dominant primary parasitoid followed by *A. tedellae*,

Table 1. Larval parasitism in *E. tedella*.

	mean %	range of %	"host" (100 %)
<i>P. dubius</i>	24.4	7.1-50.8	<i>E. t.</i>
<i>A. tedellae</i>	18.9	.8-53.7	<i>E. t.</i>
<i>A.? cingulipes</i>	1.6	.0-10.5	<i>E. t.</i>
<i>C. cursitans</i>	5.3	.6-14.3	<i>A. t.</i>
<i>E. tibialis</i>	.5	.0- .87	<i>P. d.</i>
<i>M. silvarum</i>	9.0	2.5-22.1	<i>P. d.</i>
<i>M. silvarum</i>	2.6	0.- 4.1	<i>A. t.</i>

whereas *A.? cingulipes* was either absent or rare, except in one stand where 10.5 per cent parasitism was found. Among the cleptoparasitoids, *C. cursitans* was by far the most dominant species, whereas *E. tibialis* was found only in some stands, and then in very low numbers. Only one hyperparasitoid, *M. silvarum* was found attacking both *P. dubius*, *A. tedellae* and *C. cursitans*, though *P. dubius* was the preferred host species. Fig. 3 shows a network diagram of the parasitoid-complex of *E. tedella* in North Zealand.

The frequency and outcome of multiparasitism have been studied for all species. Within this parasitoid-complex the outcome of any species composition within a host can be predicted as the results have been found to follow a general scheme. Thus, except for "rare incidents"

A. tedellae always wins when competing with *P. dubius*. The results of multi-, clepto- and hyperparasitism, and the existence of more or less random superparasitism, are shown in Fig. 4.

The quantitatively most important multiparasitism (cleptoparasitism excluded) concerns *P. dubius* and *A. tedellae*. Apparently *A. tedellae* does not discriminate between healthy hosts and those parasitized by *P. dubius*; however, due to differences in the temporal and spatial distributions of the two species, multiparasitism found on branches in one particular height was only .412 times the value expected if time and space considerations were disregarded.

Concluding remarks

In a broader population dynamic perspective, to be presented subsequently, the present parasitoid complex must be viewed as an entity with distinct spatial and temporal patterning, but subjected to modifications by interspecific influences. Still, a profound knowledge on the biology of the parasitoids is essential when realistic host-parasitoid models are to be constructed. The following relations should all be clarified: The specific behaviour of the searching females, handling time, sex-ratio, encapsulation in the host (immunity), super-, multi- and hyperparasitism as well as other relations between the parasitoids concerned, temporal aspects, spatial distribution of the attacks, searching effect, the influence of weather on ac-

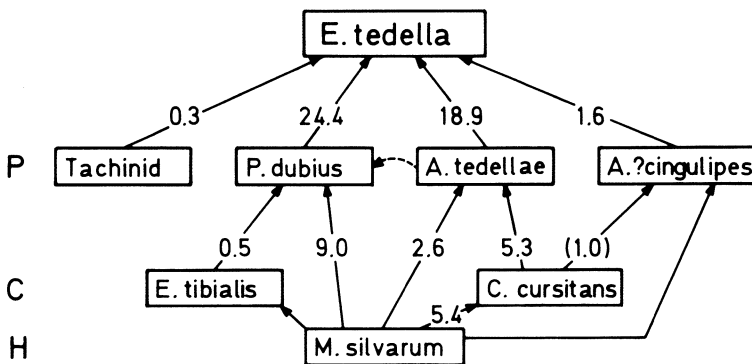


Fig. 3. Diagram of the parasitoid complex of *E. tedella*. Average values on percentage parasitism, referring to the attacked species, are given. The broken arrow indicate that *A. tedellae* is an obligate winner in case of multiparasitism.

	P. d.	A. t.	A. c.	Tach	E. t.	C. c.	M. s.
P. d.	S						
A. t.	↑	S					
A. c.	↑	-	S				
Tach	-	-	-	-			
E. t.	↑	-	-	-	S		
C. c.	↑	↑	↑	-	↑	-	
M. s.	H	H	H	-	H	H	S

Fig. 4. The competitive relations between the parasitoids of *E. tedella* as these appear within the same host individual. The arrows indicate the losing species in case of multi- and cleptoparasitism, whereas (-) represents "not observed", (S) superparasitism occurs and (H) hyperparasitism occurs.

tivity and the influence of the conditions of the locality (structure, micro-climate etc.) on searching effect.

In the previous section, observations are presented that are necessary, but so far insufficient, for the understanding of the forest-pest-parasitoid system and for correct interpretation of observed events in the dynamics of the populations.

As the long-term investigation will later show, the parasitoids of *E. tedella* are of real importance as they cause mortalities that are high compared with the low fecundity of the host, and as they have also a stabilizing effect on the system. Through the present investigation it appears that, among the parasitoids, only *P. dubius*, *A. tedellae*, *C. cursitans*, *M. silvarum* and *T. evanescens* may have a significant effect on the dynamics of the host in Denmark, and that it may be sufficient to concentrate on these five species in the modelling of parasitism of *E. tedella*.

In general, the importance of parasitoids as decimating enemies may be underestimated, as their presence apparently decreases host densities in the field by a much greater factor than that expected from common assumptions (Beddington, Free & Lawton, 1978). Further, parasitoids may assist in keeping the host population from escaping a domain of attraction at a low density level, even though the observed parasitism is not very high (Peterman, Clark & Holling, 1978).

Acknowledgements

I am grateful to Prof. E. Führer, who kindly placed his collection of parasitoids at my disposal, to O. Lomholdt for assistance with the identifications, and to Prof. C. Overgaard Nielsen, P. Holter and Dr. C. Chapman-Andresen, who read and corrected the draft of the manuscript.

References

- Beddington, J. R., Free, C. A. & Lawton, J. H., 1978: Characteristics of successful natural enemies in models of biological control of insect pests. - *Nature* 273: 513-519.
- Capek, M., 1969: Zur Problematik der Insektenparasiten des Fichtennestwicklers *Epinotia tedella* (Cl.). - *Acta Univ. Agri. Brno* 38, rada C: 271-283.
- Führer, E., 1964: Zum Auftreten des Fichtennestwicklers *Epiblema tedella* Cl. (Lep., Tortricidae) in Schleswig-Holstein. - *Z. ang. Ent.* 54: 150-163.
- , 1970: Studien über ökologische Auswirkungen der physiologischen Beeinflussung von *Epiblema tedella* Cl. durch entomophage Endoparasiten. - *Habilit. schr. Forst. Fak. Göttingen*, 247 pp.
- , 1972: Eine parasitär bedingte Entwicklungshemmung der Flügelimaginalscheiben in der Larven von *Epiblema tedella* Cl. (Lep., Tortricidae). *Z. ang. Ent.* 71: 113-120.
- , 1973: Der Einfluss zweier Endoparasiten auf die Gonadenentwicklung in der Larven von *Epiblema (= Eucosma) tedella* Cl. (Lep., Tortricidae). - *Z. Parasitenk.* 41: 187-206.
- Holling, C. S., 1959: Some characteristics of simple types of predation and parasitism. - *Can Ent.* 91: 385-98.

- Jørgensen, O. F., 1975: Competition among larvae of *Pimplouterus dubius* Hgn. (Hymenoptera: Ichneumonidae), a parasitoid of *Epinotia tedella* Cl. (Lepidoptera: Tortricidae). – Z. ang. Ent. 79: 301–309.
- Münster-Swendsen, M., 1973a: Træk af insekt-parasitoidernes biologi og værtsrelationer. – Ent. Meddr 41: 3–15.
- , 1973b: En klækkefælde og faldgrubefælde til insekt-økologiske undersøgelser. – Flora og Fauna 79: 85–92.
- & Nachman, G., 1978: Asynchrony in insect host-parasite interaction and its effect on stability, studied by a simulation model. – J. Anim. Ecol. 47: 159–171.
- Peterman, R. M., Clark, W. C. & Holling, C. S., 1978: The dynamics of resilience: Shifting stability domains in fish and insect systems. – IRE report R-15, Vancouver: 1–47.
- Schedl, K. E., 1951: Der Fichtennestwickler (*Epiblema tedella* Cl.) – Landesforstinsp. f. Kärnten: 1–136.
- Thompson, W. R., 1957: A catalogue of the parasites and predators of insect pests. – Comm. Inst. of Biol. control, Ottawa.

Sammendrag

Parasitoid komplekset hos *Epinotia tedella* (Cl.) (Lepidoptera: Tortricidae).

Som et led i en større undersøgelse af Grannåleviklerens, *Epinotia tedella* (Cl.), populationsdynamik i Gribskov, Nordsjælland, har parasitoiderne knyttet til denne art været studeret indgående igennem 9 år.

Pimplouterus dubius (Hgn.) og *Apanteles tedellae* Nix. er helt dominerende blandt primærparasitoiderne. De angribes selv af hver deres kleptoparasitoid, henholdsvis *Exochus tibialis* Hgn. og *Campoplex cursitans* (Hgn.), mens alle fire arter angribes af en hyperparasitoid, *Mesochorus silvarum* Curt. De nævnte arter er alle monovoltine og solitære endoparasitoider. *P. dubius* og *A. tedellae* kan begge betragtes som værtsspecifikke i en beskrivelse af arternes dynamik inden for en Rødgran-bevoksning.

P. dubius klækkes i perioden 10/6 til 15/7 med ca. 9 dages protandri og ♀/♂-forhold på 1,67 i gennemsnit. Den angriber 1. larvestadium fra sidst i juni til sidst i juli. Herunder fører den læggebrodden ind gennem åbningen til den mine, som værten danner i grannålene. Larver i miner, der er mere end 6–7 mm lange, kan derfor ikke nås af *P. dubius*. Arten kan ikke skelne imellem parasiterede/uparasiterede værter og fordelingen af afkom i værter følger en tilfældig fordeling (Fig. 2a). Den intraspecificke konkurrence imellem *P. dubius*-larver i samme vært afgøres gennem fysiologisk undertrykkelse.

A. tedellae klækkes i perioden 15/6 til 15/7 med ca. 9 dages protandri og ♀/♂-forhold på 1,06 i gennemsnit. Arten angriber 1. eller 2. larvestadium fra 1/7 til 1/8 og borer herunder læggebrodden direkte igennem minens væg, – en metode, der ikke fremkalder synkroniseringsproblemer. *A. tedellae* skelner ikke imellem parasiterede/uparasiterede værter og superparasiteringen følger på udvalgte grenafsnit en tilfældig fordeling (Fig. 2b), mens angrebene i større skala er aggregerede. Den intraspecificke konkurrence afgøres rent fysisk, idet mandiblerne benyttes som våben.

M. silvarum klækkes i perioden 15/6 til 15/7 med ca. 7 dages protandri. Den anbringer sine æg i parasitoid-larver, placerede i deres vært, og angriber hyppigst *P. dubius*. Superparasitering finder sted.

C. cursitans klækkes i perioden 20/6 til 25/7 med ca. 8 dages protandri. Arten er obligatorisk kleptoparasitoid, idet den udelukkende angriber *E. tedella*-larver, der allerede er parasiterede af *A. tedellae*. Larven findes forrest i værtens hæmocoel og dræber altid *A. tedellae* gennem fysiologisk undertrykkelse. Superparasitering er ikke observeret.

E. tibialis angriber tilsvarende kun værter, der allerede er parasiterede af *P. dubius* og dræber formentlig sidstnævnte ved brug af mandiblerne. Superparasitering finder sted.

Et diagram over parasitoid komplekset, med angivelser af gennemsnitlige parasiterings procenter er vist på Fig. 3. Når *A. tedellae* og *P. dubius* tilfældigvis er til stede i samme vært, dræbes sidstnævnte altid. Et skema over multiparasitære relationer som denne er vist i Fig. 4.