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Partial Appearance of Non-hibernating Adults and Egg Complements in the Poplar Sawfly *Trichiocampus populi* (Hymenoptera, Tenthredinidae)[1]

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Abstract The partial appearance of non-hibernating adults of the poplar sawfly *Trichiocampus populi* in the late summer to early fall is described. Their percentage ratio attained 11.2% of total individuals in 1978, but they never appeared in 1979, indicating an erratic nature of the appearance.

In both hibernating and non-hibernating adults the sex ratio is highly skewed, the males occupying only one fourth or less. The egg complements of hibernating and non-hibernating females five days after emergence are respectively about 120 and 150. About 87.4 and 86.2% of these ovarian eggs are already mature at emergence. The egg complement positively correlates with wing length. A slight but significant difference is found between hibernating and non-hibernating females, in the latter wings being relatively shorter but the egg complement larger. The possible ecological significance of these findings are briefly discussed.

Introduction

The poplar sawfly *Trichiocampus populi* Okamoto is fairly common in and near Sapporo, but its outburst resulting in a serious defoliation has never been recorded. This implies that its populations are maintained at a certain density level from year to year by intervention of some mortality factors. The life cycle of *T. populi* is divided into a very short feeding period and a long inactive period, which lasts, ignoring the partial first generation reported below, from late August to the next July, the most part of which is spent by prepupae with a remarkable frost resistance (1). Apparently the mortality factors should differentially operate on these two periods. The present paper reports the partial appearance of non-hibernating adults and the egg complement of adult females, as the first attempt to apprehend the life cycle schedule of this species.

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Materials and Methods

The mature larvae leaving the foliage and wandering on the trunks of poplar trees or on the ground nearby the feet were collected during August to September in 1978 and 1979. The dry stems of the composite weed *Rudbeckia laciniata* were cut in 5~10 cm long and given as hibernacula (1). As given below, in 1978 a small fraction of adults emerged within the year (=non-hibernating individuals, H′), but the majority emerged in the next year during June to August, mostly in July (=hibernating individuals, H). In both groups the adult females were dissected either soon after emergence or several days (mostly five days) later (=H'_0, H'_5 August 30~ September 5, 1978; H_0, H_5 June 28~ July 13, 1979), and the numbers of ovarioles, mature ovarian eggs, and oocytes, the length of which exceeded the half length of mature eggs, were counted for each ovary separately. For each individual the length of the right fore wing including tegula was measured as an index of body size.

Results

Partial occurrence of non-hibernating individuals and the related problems: During the course of studies on the frost resistance of *T. populi*, one of us (T. K.) has noticed a small number of mature larvae wandering at or near the feet of poplar trees at the end of September, apparently much later than the peak of wandering from late August to early September. That these later mature larvae are the offsprings of some H′ adults was confirmed in 1978 by the emergence of 116 adults during August 29~ September 11 (50% emergence on Sept. 1) from the sample collected during mid August~ early September. Thereafter, the hibernacula were kept in a non-heated outdoor room and the contents were examined at the end of May (Table 1), i. e. before the burst of emergence which took place mostly in mid June (2).

Among the individuals of various conditions found in hibernacula the following ones indubitably belong to H: R_a, R_{ds} (=relatively recently died), R_{dp} (this unidentified parasitic fly emerges in the fall), P_a and A_a (representing the starts of pupation and emergence). Most if not all of P_d and A_d may belong to H′ because their dried corpses suggest the earlier deaths. Most R_{dl} may belong to H though the occurrence of a fraction of H′ is not precluded. As a first approximation we estimate the number of H′ individuals at 166 (=P_d+A_d+No. emerged adults), i. e. about 11.2% of total individuals collected (=1,479). In 1979, however, no adult emerged before the winter from the sample of 734 individuals which entered in hibernacula during August to September.

In early to mid September 1978 a small number of larvae evidently born of H′ females were discovered. All 76 first to second instar larvae

Table 1. Contents of hibernacula examined at the end of May 1979

Condition	Female	Male	Total
Prepupa (R)	947	334	1,308
Alive (R_a)	685	152	837
Dead (R_d)	289	182	471
Soft (R_{ds})	27	4	31
Solidified (R_{dl})	229	162	391
Parasitized (R_{dp})	33	16	49
Parasite emerged	24	12	36
Parasite dead	9	4	13
Pupa (P)	13	2	15
Alive (P_a)	3	—	3
Dead (P_d)	10	2	12
Adult (A)	32	8	40
Alive (A_a)	—	2	2
Dead (A_d)	32	6	38
Total	1,019	344	1,363
H′ emerged in 1978	86	30	116

of this partial first generation (G_1) reared in laboratory succumbed a few days later. Fify five first instar G_1 larvae were daily observed on the field but all died or lost within 17 days. Among 43 last instar G_1 labo-reared larvae, 23 entered in hibernacula and 12 adults (6♀+5♂) emerged in the next year.

Table 1 also contains some mortality data during the inactive period. But here is mentioned only a very skewed sex ratio in this species. For the individuals collected in 1978, the males occupied only 22.9% (38/166×100) in H′ and 25.6% (336/1, 313×100) in H. In 1979 no H′ was obtained. The sexes are distinguished by the size of head capsule in the last instar larvae. Among 734 larvae entered in hibernacula, the males occupied only 22.5%.

In 1978 some H′ adults were isolately reared either in a small plastic box provided with poplar leaves, a piece of moisten cotton and a cotton piece dipped with diluted honey (A) or in a cotton-stopped vial with no food and moisture (B). The life span of these adults were:

No. survived since emergence

Day	1	2	3	4	5	6	7	8	9	50% survival
A♀	38	38	35	28	20	17	5	2	0	5.3 days
A♂	6	6	5	5	4	3	2	0	—	6.0 days
B♀	23	23	22	18	14	8	3	1	0	5.4 days

The result indicates that after emergence the adults survive about one week irrespective of taking food or not. Consequently the females dissected five days after emergene (H_5, H'_5) are regarded as showing the full egg complement.

Egg complement and other ovarian features: The egg and ovaries of this speces were described by Iwata (3, 4). Eggs are milky white, about 1.1 mm long and 0.3～0.4 mm wide, slightly narrowed toward the cephalic pole, one side is distinctly convex while the other side rather straight or gently concave. The ovaries contain numerous mature eggs at emergence. Among the results given in Table 2, the most important figures concerning the population trend are obviously $\bar{E}_t$ in both H and H′ but some other obtained relations are also briefly referred to.

1. *The left-right symmetry*: Based upon the null hypothesis $\bar{\Delta}=1-r=0$, the results of *t*-test showed no significant differences except the following cases:

Table 2. Mean number of mature ovarian eggs ($\bar{E}$), half-grown oocytes ($\bar{O}$) and ovarioles ($\overline{Ol}$) in ovaries and mean length of right wing ($\overline{W}$, mm)

Group	H_0	H_5	H'_0	H'_5
n	55	50	10	10
$\overline{W}$	8.20	8.32	7.88	8.00
SD	0.42	0.32	0.13	0.28
Left ovary				
$\bar{E}_l$	47.9	60.1	50.7	75.8
SD	16.2	13.8	11.6	9.3
$\bar{O}_l$	11.2	2.4	18.1	8.1
SD	4.4	1.7	6.8	1.0
$\overline{Ol}_l$	22.0	21.5	20.7	21.2
SD	2.4	2.4	1.3	1.2
Right ovary				
$\bar{E}_r$	48.1	60.8	48.3	74.9
SD	16.8	13.8	14.3	13.1
$\bar{O}_r$	11.0	4.5	18.6	7.7
SD	4.2	2.0	7.6	1.9
$\overline{Ol}_r$	21.1	21.8	19.6	20.6
SD	2.5	2.8	2.5	0.8
Total				
$\bar{E}_t$	95.9	120.9	99.0	150.7
SD	32.2	26.6	24.2	21.2
$\bar{O}_t$	22.1	6.8	36.7	15.8
SD	8.2	2.9	13.8	2.0
$\overline{Ol}_t$	43.1	43.3	40.3	41.8
SD	4.4	4.7	3.1	1.8

H_0, $\overline{\mathrm{Ol}}_l-\overline{\mathrm{Ol}}_r$ $(=-0.9\pm3.3,\ P<0.1)$; H_5, $\bar{\mathrm{O}}_l-\bar{\mathrm{O}}_r$ $(=-2.1\pm2.2,\ P<0.001)$; H'_0, $\overline{\mathrm{Ol}}_l-\overline{\mathrm{Ol}}_r$ $(=1.0\pm2.7,\ 0.3>P>0.2)$; and H'_5, $\overline{\mathrm{Ol}}_l-\overline{\mathrm{Ol}}_r$ $(=0.6\pm1.0,\ 0.2>P>0.1)$.

Probably these deviations were caused by observational errors. As the female metasoma is full of easily detaching mature eggs, occasional confusion between left and right fractions is not precluded.

2. *Differences between age groups and* $H\sim H'$: According to the results of *t*-test (Table 3), both wing length and number of ovarioles are slightly larger in HH'_5 than in HH'_0, though the difference is statistically insignificant in H. Generally but not strictly HH'_0 were dissected chronologically earlier than HH'_5. The results might show an earlier emergence of females with larger wings and more developed gonads.

The differences in $\bar{\mathrm{O}}_t$ and $\bar{\mathrm{E}}_t$ are highly significant and inversely correlated. Evidently this indicates the post-emergence development of some large oocytes into mature eggs. Assuming a random selection of individuals between HH'_0 and HH'_5, which may not always be true as mentioned above, $\bar{\mathrm{E}}_{t.5}$ is given by

$$\bar{\mathrm{E}}_{t\cdot5}=\bar{\mathrm{E}}_{t\cdot0}+(\bar{\mathrm{O}}_{t\cdot5}-\bar{\mathrm{O}}_{t\cdot5})\,.$$

The value $(\bar{\mathrm{O}}_{t\cdot0}-\bar{\mathrm{O}}_{t\cdot5})$ is 15.3 in H and 20.9 in H′ or 12.6 (15.9) and 13.8 (21.1%) of $\bar{\mathrm{E}}_{t\cdot5}$ $(\bar{\mathrm{E}}_{t\cdot0})$ respectively. These figures are regarded as the provisional estimated for the number of mature eggs added to total egg production after emergence. Evidently the majority of eggs are already fully grown at emergence.

Among H and H′ a tendency $H>H'$ in $\overline{\mathrm{W}}$ and $\overline{\mathrm{Ol}}$ and $H'>H$ in $\bar{\mathrm{O}}_t$ and $\bar{\mathrm{E}}_t$ are recognized, though the difference is statistically insignificant in $\overline{\mathrm{Ol}}_t/HH'_5$ and $\bar{\mathrm{E}}_t/HH'_0$. The reproductive efficiency per ovariole $(\bar{\mathrm{E}}_t+\bar{\mathrm{O}}_t)/\overline{\mathrm{Ol}}_t$ is higher in H′ than H (H'_0 3.37, H'_5 3.98; H_0 2.74, H_5 2.95). These tendencies may indicate a differential investment of food to somatic and repro-

Table 3. Significance in diferences of measured characters between age groups and $H\sim H'$

character group	DF	$\overline{\mathrm{W}}$	$\overline{\mathrm{Ol}}_t$	$\bar{\mathrm{O}}_t$	$\bar{\mathrm{E}}_t$
$H_0\sim H_5$	103	$-\ H_5\geq H_0$ *t*: 0.67453 $0.6>P>0.5$	$-\ H_5\geq H_0$ *t*: 0.66909 $0.6>P>0.5$	$+\ H_0\gg H_5$ *t*: 12.38231 $P<0.001$	$+\ H_5\gg H_0$ *t*: 4.23736 $P<0.001$
$H'_0\sim H'_5$	18	$\pm\ H'_5>H'_0$ *t*: 1.16615 $0.3>P>0.2$	$\pm\ H'_5>H'_0$ *t*: 1.25534 $0.3>P>0.2$	$+\ H'_0\gg H'_5$ *t*: 4.49650 $P<0.001$	$+\ H'_5\gg H'_0$ *t*: 4.83074 $P<0.001$
$H_0\sim H'_0$	63	$+\ H_0>H'_0$ *t*: 2.8736 $P<0.01$	$+\ H_0>H'_0$ *t*: 2.43949 $P<00.2$	$+\ H'_0>H_0$ *t*: 4.50352 $P<0.01$	$-\ H'_0\geq H_0$ *t*: 0.28502 $0.9>P>0.8$
$H_5\sim H'_5$	58	$+\ H_5>H'_5$ *t*: 2.89534 $P<0.01$	$-\ H_5\geq H'_5$ *t*: 0.97803 $0.4<P<0.3$	$+\ H'_5>H_5$ *t*: 9.22043 $P<0.001$	$+\ H'_5>H_5$ *t*: 3.30300 $P<0.01$

ductive fractions, possibly more to somatic fraction in H and *vice versa* in H′.

3. *Correlation between $\overline{W}$ and three ovarian features*: Between $\overline{W}$ and $\overline{Ol}_t$, $\bar{O}_t$, $\bar{E}_t$, significant correlation was found in $\overline{W} \sim \bar{E}_t$ of all four groups. As to $\overline{W} \sim \overline{Ol}_t$ and $\overline{W} \sim \bar{O}_t$ the correlation was positive in H_0 ($r=0.6345$), H_5 ($r=0.7584$), H'_5 ($r=0.8170$) but negative in H'_0 ($r=-0.6401$). The negative correlation in H'_0 is difficult to explain. In this group, however, the variation of wing length is small (Table 2, $SD=0.13$). Possibly this sample covered the size range incompletely and casually showed a negative correlation.

Fig. 1 depicts the relation between wing length and total number of mature eggs in H'_5 and H_5. The regression line is $\bar{E}_t=9.21\overline{W}-586.44$ for H'_5 and $\bar{E}_t=10.63\overline{W}-764.26$ for H_5, evidently showing a higher reproductive capacity in H′ than in H.

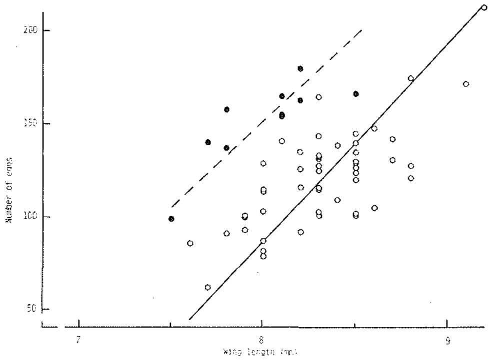

Fig. 1. Relation between wing length and number of mature ovarian eggs in *T. populi* (H_5 ○——, H'_5 ●⋯⋯)

Discussion

The appearance of some non-hibernating adults in the later summer to early fall gives a complication to the life cycle of *Trichiocampus populi.* But its low and unstable ratio, 11.2% in 1978 and 0.0% in 1979, suggests its erratic nature, probably appearing as a byproduct of changes of some environmental factors. Possibly thermal conditions affect the incidence either directly or indirectly via daytime length. It was confirmed that these H′ females can produce the partial first generation (G_1), and that such G_1 adults can emerge in the next early summer together with H ($=G_0$) adults. To what extent these G_1 adults contribute to the population fluctuation should be clarified by further studies. But its contribution seems not much large, judging from its low and erratic ratio and its possibly low survival in the later fall as suggested above.

The ovarian features of *T. populi* do not much differ from those of other nematine species, which possess a relatively large number of ovarioles (10～30 per ovary) and mature ovarian eggs (30～2000) among Symphyta (4).

The correlation between body size and egg complement is also known in many other insects, e. g. in sawflies in *Perga affinis affinis* (5). As in this species and in many other sawflies the females of *T. populi* virtually do not feed after emergence. Hence, the body size, and the consequent egg complement are ultimately mediated by the factors affecting the amount of food ingested in the prior year. However, the difference between H' and H indicates a differential partition of food into somatic and reproductive investments (S and R), S/R being H>H'. The hibernating females evidently lose the stored matter during the prolonged quiescent period. For instance, the prepupae lose about 12.2% of body weight during the diapause lasting seven months (1). If the emergence occurs without prolonged diapause the wing length could increase much. Assuming the prepupal body weight being simply proportional to $\overline{\mathrm{W}}^3$, the diffierence of 12.2% given above is equivalent to 2.3% in $\overline{\mathrm{W}}$. The actual percentage difference in wing length, $(\overline{\mathrm{W}}_{\mathrm{H}5}-\overline{\mathrm{W}}_{\mathrm{H'}5})/\overline{\mathrm{W}}_{\mathrm{H}5}\cdot 100$ is 3.8%, the amount approximately of the comparable order. In *T. populi* the majority of eggs are fullgrown at emergence as in many Symphyta groups. The additional increase during the short adult stage without food intake is 16~21%. The mortality factors operating on the adult stage may practically not affect the ratio, as these factors synchronously decrease the number of mature eggs to be laid.

The egg complement of *T. populi*, about 120 in H and 150 in H', is not so large among insects. Nevertheless, in order to keep a stable population level, a considerable portion of individuals should succumb before attaining the reproductive stage. Ignoring the partial occurrence of H' and assuming the absence of any pre-reproductive mortalities, the individual number of the second generation (N_2) is estimated by,

$$N_2 = N_1\cdot\bar{\mathrm{E}}_{\mathrm{t}}\cdot f(f+m),$$

where N_1 denotes the individual number of the first generation, and f and m the number of females and males. Adopting the values $\bar{\mathrm{E}}_{\mathrm{t}}=120.9$ and $f(f+m)=0.7744$, then $N_2=93.625\ N_1$. To have the equilibrium $N_1=N_2$, about 98.93% of individuals should be removed from the population during the pre-reproductive stages. The incorporation of the partial non-hibernating females into the picture is given by,

$$\begin{aligned}N'_2 = {} & N_1\cdot\hat{\mathrm{H}}/(\hat{\mathrm{H}}+\hat{\mathrm{H}}')\cdot\bar{\mathrm{E}}_{\mathrm{tH}}\cdot f_{\mathrm{H}}/(f_{\mathrm{H}}+m_{\mathrm{H}})\\ & +N_1\cdot\hat{\mathrm{H}}'/(\hat{\mathrm{H}}+\hat{\mathrm{H}}')\cdot\bar{\mathrm{E}}_{\mathrm{tH'}}\cdot f_{\mathrm{H'}}\,(f_{\mathrm{H'}}+m_{\mathrm{H'}})\cdot\bar{\mathrm{E}}_{\mathrm{tH}}\cdot f_{\mathrm{H}}/(f_{\mathrm{H}}+m_{\mathrm{H}}),\end{aligned}$$

where N'_2 is the individuals produced by both H and H' adults emerging in the next summer, H and H' denote the individual numbers of $\hat{\mathrm{H}}$ and $\hat{\mathrm{H}}'$ adults emerging in the late summer, and $\bar{\mathrm{E}}_{\mathrm{tH}}$, $\bar{\mathrm{E}}_{\mathrm{tH'}}$, etc. the values corresponding to H and H'. Assuming the sex ratio and egg complement of the partial first generation (G_1) as equal to those in G_0 (=ordinary hibernating adults),

$$N_2' = 83.1390N_1 + 1218.3647N_1 .$$

To keep the equilibrium $N_1 = N_2'$, 99.92% should be eliminated pre-reproductively. The second item of the equation shows a drastic increase of the expected number of individuals by the occurrence of partial H′, provided the pre-reproductive mortality of the offsprings of H′ is assumed to be zero. Certainly the pre-reproductive mortality in these partial G_1 individuals, the feeding period of which covers the unfavorable fall season, should be quite high.

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