ハイイロハリバエのマツカレハに対する寄生の周年経過

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論　文

Annual Cycle of Parasitism to the Pine Moth, *Dendrolimus spectabilis* BUTLER, by a Tachinid Fly, *Carcelia bombylans* R.-D.

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KAWANISHI, Michiharu: **Annual cycle of parasitism to the pine moth, *Dendrolimus spectabilis* BUTLER, by a tachinid fly, *Carcelia bombylans* R.-D. J. Jap. For. Soc. 60: 442～449, 1978** The larvae and cocoons of the pine moth were collected periodically and were reared in the laboratory. They were used for the examination of the periods of fly emergence. The periods of attack by the adult fly were determined through some additional field experiments. The flies laid their eggs on the young moth larvae from early September, when the 1st instar host larvae appeared in the field, up to late October. Most of the fly larvae which penetrated the host larvae in this period overwintered in the host. They emerged from the 6th and the 7th instar host larvae from late April to late May. Thereafter, the fly parasitized the moth larvae by mid-June and emerged from the prepupal stage of the host from mid-July to mid-August. But the fly didn't parasitize the fully grown host larvae after mid-June, although adult flies existed in the field. The fly also attacked the host cocoons after mid-July, and caused heavy mortality upon the host pupae. The annual cycle of the parasitism by the fly, together with the relation to other hosts, was proposed in a schematic diagram.

川西通晴: **ハイイロハリバエのマツカレハに対する寄生の周年経過　日林誌 60: 442～449, 1978**　マツカレハ幼虫・繭の定期的採集と飼育および野外実験・観察にもとづき，ハイイロハリバエの産卵攻撃と寄主からの脱出の周年経過を調査した。ハリバエ成虫はマツカレハ1齢幼虫が出現する9月上旬から10月下旬にわたって寄主幼虫に産卵攻撃した。この期間に寄主体内に侵入したハリバエ幼虫の大部分はそのまま越冬し，翌春4月下旬～5月下旬に寄主の6，7齢幼虫から脱出した。その後ハイイロハリバエは，6月中旬までに再びマツカレハ幼虫に寄生し，7月中旬以降に寄主の前蛹期に脱出した。6月中旬以降，野外にハリバエ成虫の存在が確認されたにもかかわらず，本種のマツカレハ老熟幼虫に対する寄生は認められなかった。しかし，本種は7月中旬以降マツカレハ繭に産卵攻撃し，寄主の高い死亡率をもたらした。マツカレハに対するハイイロハリバエの寄生の周年経過が，ハリバエと他寄主との関係を含めて，図式的に示された。

I. Introduction

It is reported that the tachinid fly, *Carcelia bombylans* R.-D., causes heavy mortality to the pupal stage of the pine moth, *Dendrolimus spectabilis* BUTLER (KOKUBO, 1965; KURANAGA, 1975). The tachinid fly also emerges from the larval stage of the pine moth (NOBUCHI, 1962; KOKUBO, 1964a, 1968; IGARASHI, 1972; KAWANISHI, 1975).

Although this tachinid fly is one of the most important mortality factors of the pine moth, there has been no intensive survey of the host-parasite relationship between them.

In a previous report (KAWANISHI, 1975), the parasitism by this tachinid fly from spring to summer was clarified to some extent, but the parasitism from summer to autumn remained uncertain. Thus, as a next step, it was necessary to pursue in detail the fly's parasitic activity in relation to the progress of season and to the stages of the host moth. In this report, the author describes the annual cycle of the parasitism to the pine moth by this tachinid fly, based on the survey carried out in 1973～75 in Nagoya.

II. Materials and Methods

1. Survey of the moth larvae and cocoons in natural condition

Larvae and cocoons of the pine moth were col-

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lected periodically on pine trees in the campus of Nagoya University in Nagoya City. The larvae were reared on Japanese red pine (*Pinus densiflora*) leaves, and were kept in groups of 5～30 in containers which were 15 cm in diameter and 9 cm in height. These containers were placed near the window where they were not exposed to the direct sun, and the daylight was maintained at its natural length. The larvae of the fly killed the host larvae 1 or 2 days before they emerged from the host. Since one of the purposes of this report was to determine the number of parasites emerging per host, each of the newly dead host larvae was removed from the containers and transferred separately into a plastic cup (9 cm in diameter and 5 cm in height). Dates and numbers of the emerging flies and the periods of their puparium stage were recorded in the cup. When they reached the adult, they were transferred into a cage ($20 \times 20 \times 15\,cm^3$) of nylon gauze supplied with a small cup containing a piece of cotton moistened with 10% hcney solution, and their life span was measured.

In a pine stand (composed of 53 trees with 2～4 m in height, and $70\,m^2$ in area) in the nursery of Nagoya University campus, the number of cocoons of the pine moth was counted at 5～10-day intervals. On each census day newly spun cocoons were numbered and all the cocoons were examined by using tweezers to see whether the pupae or prepupae in them were alive or not. If they were dead, the mortality factor was deter mined by dissection.

2. Field parasitism to the reared moth larvae

In 1974, the unparasitized moth larvae of the final instar reared in the laboratory were placed on pine trees in the nursery on June 15th, and were collected after spinning of the cocoons on June 28th and July 4th. They were placed in cups separately and the number of parasites emerged per host was recorded.

In 1975, the unparasitized moth larvae of 2nd and 3rd instar were released on the same trees on September 11th and collected on November 21st. They were reared in the laboratory and were examined later to determine whether they were parasitized or not.

3. Developmental course of the pine moth

In order to get more detailed information about the developmental course of the moth than that obtained through field observation, a rearing experiment was carried out under laboratory conditions. Twenty-five larvae of the pine moth which hatched on August 28th, 1974, were reared separately on Japanese red pine leaves in glass tubes (3 cm in diameter and 20 cm in length) until overwintering, and thereafter they were kept separately in the plastic cups until they pupated, and their total development was thus recorded.

III. Results

1. Field observations for the life history of the pine moth in Nagoya

The pine moth had one generation a year. The adult moths appeared in August and they mated and laid their eggs just after the emergence from their pupae. The eggs hatched in 7～10 days and the first instar larvae began to feed on pine needles from late August to early September, and the next spring they resumed feeding on pine needles in late March. The fully grown larvae set in spinning their cocoons about July 10th and pupated with prepupal stage of 2 to 3 days.

Figure 1 shows the distribution of the head width of the larvae collected in the field on December 28th, 1974. These larvae were considered to be the 4th to 6th instar on the basis of the measurement by YAMADA (1964).

2. Rearing experiment

The result shown in Fig. 1 corresponds with that of the laboratory rearing experiment of 25

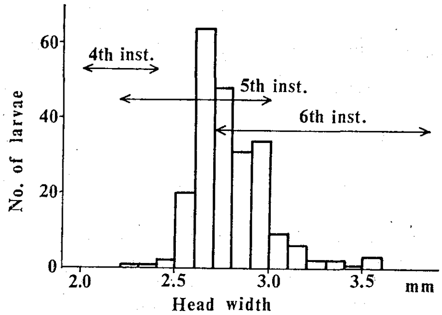

Fig. 1. Frequency distribution of the head width of the larvae of the pine moth collected in the field on December 28th, 1974
Arrows indicate the ranges of the head width of each instar on the basis of the measurement by YAMADA (1964).

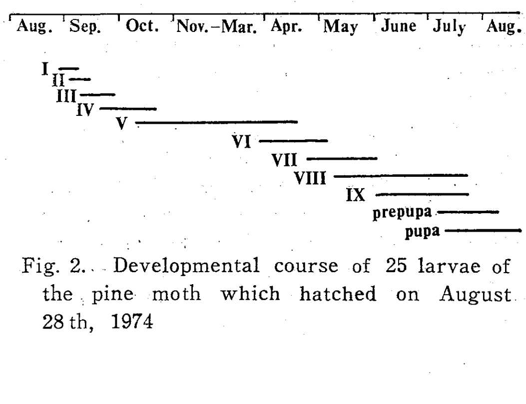

Fig. 2. Developmental course of 25 larvae of the pine moth which hatched on August 28th, 1974

Table 1. Seasonal trends of the parasitism of *C. bombylans* to the moth larvae

Date of collection	No. of collected larvae	No. of parasitized larvae	Parasitism (%)	Period of emergence	Host stage*	Range of P/H (mean)
July 1, 1973	80	25	31.3**	July 14~Aug.5	prepupa	1~4(1.8)
July 15	40	10	25.0**			
Apr.3~5, 1974	316	52	16.5	Apr.22~May 2	6th instar	1
		27	8.5	May 3~18	7th instar	1
		79	25.0			
May 6	140	6	4.3	May 7~15	6th instar	1
		12	8.6	May 10~23	7th instar	1
		18	12.9			
June 16	124	20	16.1***	mid-July~early Aug.	prepupa	1~4
July 20	34	5	14.7***	mid-July~early Aug.	prepupa	1~4
Dec.28	164	71	43.3	Apr.18~May 16	6~7th instar	1
Apr.11, 1975	169	54	32.0	Apr.20~May 2	6th instar	1
		39	23.1	May 1~17	7th instar	1
		93	55.1			
June 9	19	3	15.8	mid-July~late July	prepupa	1~2
July 5	32	8	25.0	mid-July~early Aug.	prepupa	1~4(1.9)
Sep.11	46	2	4.3	Sep.28 and Oct.2	4th instar	1
		14	30.4	late Nov.~Jan.****	—	1
		16	34.7			
Oct.6	47	22	46.8	Dec.~Jan.****	—	1
Nov.21	345*****	67	19.4	Dec.~Jan.****	—	1

P/H: emergence numbers of parasites per host
* Host stages at the emergence of parasite larvae ** $\chi_0^2=0.504$ ($0.30<P<0.50$)
*** $\chi_0^2=0.041$ ($0.80<P<0.90$) **** incubated in the rearing room
***** They were exposed to field conditions after Sep.11

Table 2. Parasitism to the moth cocoons by *C. bombylans* over three years

Year (date of collection)	No. of collected cocoons	No. of parasitized prepupae and pupae		Parasitism (%)	P/H*	
					Range	Mean
1973 (Aug.1~4)	274	prepupa	91	32	1~4	
		pupa	164	90**	1~26	4.9
1974 (Aug.2)	160	prepupa	31	19	1~4	
		pupa	74	58**	1~22	5.2
1975 (July 23~31)	78	prepupa	23	30	1~4	2.4
		pupa	27	49**	1~19	5.9

* Emergence numbers of parasites per host
** Calculated by the following formula,

$$\frac{\text{No. of parasitized pupae}}{(\text{No. of collected cocoons})-(\text{No. of parasitized prepupae})}$$

larvae as shown in Fig. 2. These reared larvae began to overwinter at the stage of the 5th instar, and one larva was dead after overwintering. When the reared larvae reached the 7th instar, they showed the colour characteristic to late larval stages ranging from silver-gray to deep orange, which was used provisionally to distinguish the 6th from the 7th instar. As shown in Fig. 2, the larvae reached the final instar by mid-June; 17 individuals out of 24 reached the 9th instar and 7 to the 8th.

3. Emerging periods and the host stage

The field collection of the host showed that the tachinid flies emerged from the 4th, 6th and 7th instar larvae, the prepupae and the pupae of the moth, as shown in Table 1 and 2. Out of 16 individual flies that emerged from the host larvae collected on September 11th, 1974, only two emerged in autumn and the others in winter in the rearing room. Thus, most of the fly larvae that had penetrated the host body by early September seemed to overwinter in the host larvae. Therefore, the peak of the emergence from the moth was twice a year. The fly larvae emerged from the 6th to 7th instar hosts between late April and late May, and from the prepupa to pupa between mid-July and mid-August.

The emergence number of parasites per host (P/H) was 1 for 4th, 6th and 7th instar larva of the host, 1 to 4 for the prepupa and 1 to 26 for the pupa.

The frequency distribution for the number of daily emergence of flies between late April and late May was bimodal and each mode corresponded with the emergence from the 6th and 7th instar larvae of the host respectively (Fig. 3).

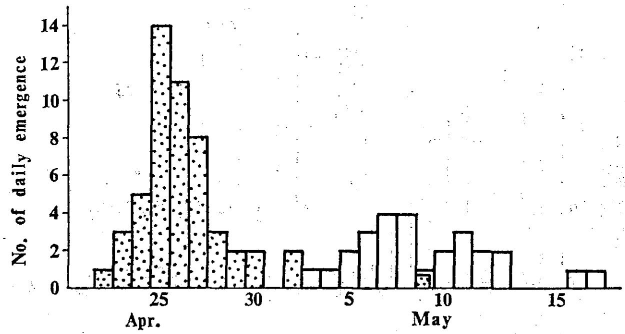

Fig. 3. Trends in the number of the daily emergence of fly larvae (*C. bombylans*) between late April and late May

Dotted bars and open bars represent the emergence from the 6th and 7th instar host larvae respectively.

The larvae of the fly pupated in 24 hours after their emergence from the host. The adult fly emerged from its puparium in about 10 days after pupation, so that most of the adult flies which came from the 6th and 7th instar host larvae might appear in the field by the end of May at the latest. Under the condition of the rearing cage, the life span of the adult fly was 12 days at the longest and it mostly ranged from 7 to 10 days.

4. Periods of attack of the adult fly

As shown in Table 1, the moth larvae collected on September 11th and the unparasitized larvae exposed to the field condition from September 11th to November 21st, 1975, were parasitized by the fly. And also, the attack of the adult fly to host larvae was observed frequently in the field until late October. These facts indicate that the fly laid eggs on the surface of the moth larvae from early September, when the 1st instar larvae of the host appeared, up to late October continuously. The fly larvae penetrated the host larvae and passed the winter in the host. From the host larvae collected on December 28th, 1974, the fly emerged during the period of mid-April to mid-May of the next year, which indicated that the fly had already been in the host larvae in the previous autumn. This conclusion was also supported by the fact that in the incubated rearing condition the fly emerged mostly in January from the larvae that had been collected on October 6th and November 21st of the previous year.

From the host larvae collected on May 6th, 1974, no fly emerged after May 23rd, or after the last date when all the flies parasitizing in the previous autumn had emerged (Table 1), which suggested that the attack to the moth larvae didn't occur from March to April.

Throughout the three years of survey, the fly emerged only from the prepupal stage of the host whose larvae were collected in June and July (Table 1). But, as shown in Table 2, the fly emerged both from the prepupae and pupae in the cocoons collected in the field from late July to early August.

If the flies were to attack the fully grown moth larvae just before spinning the cocoon, they must emerge after pupation of the host. But such individuals were not obtained. From the fully grown moth larvae of the final instar collected from July 15th to 20th, the fly did not emerge from the pupal stage (Table 1). This fact indicated that the flies emerging from the host pupae were those derived from the eggs laid directly on the host cocoons.

Table 2 shows that percentage of parasitism to the pupae was much higher than that to the prepupae every year. As shown in Fig. 4, frequency distributions of the emergence number of parasites per host prepupa and per pupa were different from each other.

There were no significant differences in the parcentage of parasitism between the larvae collected on July 1st and July 15th, 1973 and between those collected on June 16th and on July 20th, 1974. Therefore, it is presumed that the fly could not parasitize the moth larvae in the periods between July 1st and July 15th in 1973 and between June 16th and July 20th in 1974. So, the adult fly might have stopped attacking the host larvae by mid-June after the spring emergence. This reasoning is also supported by the fact that the moth larvae collected on June 9th, 1975 had already been parasitized and killed later at the prepupal stage.

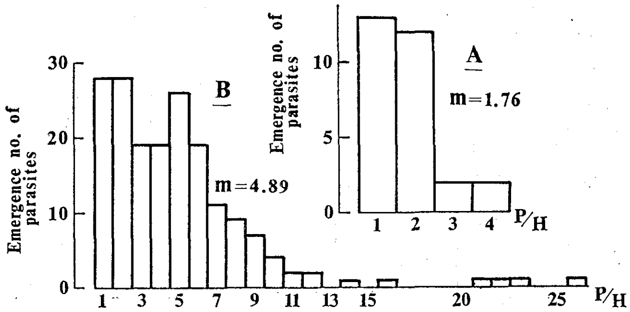

Fig. 4. Frequency distribution of the emergence number of parasites per host prepupa (A) and per host pupa (B) in 1973

Table 3. Parasitism of *C. bombylans* to the moth cocoons whose unparasitized larvae just before pupation were released on field pine trees on 15th June 1974

Date of collection	No. of collected cocoons	No. of parasitized cocoons	Parasitism (%)	Host stage*	P/H** Range	P/H** Mean
June 28	136	97	71	pupa	1～12	4.5
July 4	59	41	70	pupa	1～16	5.3
	195	138	71			

* Host stages at the emergence of parasite larvae
** Emergence numbers of parasites per host

Table 3 shows the result of the field experiment in which the unparasitized fully grown moth larvae, which were about two weeks in advance of the development of those under natural conditions, were placed on pine trees on June 15th and collected after spinning of cocoons on June 28th and July 4th. The fly emerged only from the pupa. The percentages of parasitism and P/H were similar to those observed on the cocoons collected on August 2nd of the same year (Table 2). The parasitism reached about 70%. Therefore, a good number of adult flies would have to exist in the field in the period from June 15th to July 4th to cause such a high parasitism as observed on the pupae collected on August 2nd.

Considering that the fly might attack the host larvae up to mid-June, and that the fly emerged only from the pupa (Table 1 and 3), one can deduce that the fly cannot successfully parasitize the fully grown host larvae after mid-June, although it can attack the host cocoons.

IV. Discussion

The present survey showed that the tachinid fly parasitized the pine moth in the same manner every year, emerging from particular host stages and in particular periods. All the flies that had lived within the host larvae after spring emerged from the host prepupal stage, whose period covered only a few days. This indicates a mutual relation between the emergence of the fly larva and the host stage. The bimodal distribution of the spring emergence also seems to show a close relation of the fly emergence to the host stage, but the relation is not decisive.

IGARASHI (1972) reported on the basis of his laboratory experiment that the adult fly of *C. bombylans* tried to lay eggs on every stage of the larvae of the pine moth, but they couldn't lay eggs effectively on the surface of the large larvae because of the defensive behaviour. The fact that the fly didn't parasitize the moth larvae after mid-June can be reasonably explained thus: the moth larvae had already reached the final instar by mid-June (Fig. 2), so that the adult flies couldn't lay their eggs successfully on them, nor find the host larvae in moulting, on which the fly could easily lay their eggs.

IGARASHI (1972) also pointed out that the adult fly laid many eggs on the surface of host cocoons, but when the eggs were laid on the surface of the cocoon in which the host had already pupated, the fly larvae hatching from the eggs couldn't penetrate into the host body. That is, the period when the fly can parasitize seems to be limited only to a few days between spinning of the cocoon and pupation. Table 4 shows the percentage of parasitism to the moth pupa whose larva spun its cocoon

Table 4. Parasitism of *C. bombylans* to the moth pupae whose larvae spun their cocoons in a census plot in 1974

Census day	No. of newly spun cocoons*	No. of parasitized pupae	Parasitism (%)
June 22			
	2	1	50
July 8			
	5	3	60
July 15			
	28	18	64
July 22			
	53	43	81
July 27			
	30	24	80
Aug. 4			
	3	2	66
Aug. 13			
	121	91	75

* The cocoon in which the host died at the prepupal stage is not included.

between each census day in the census plot in 1974. In this table the number of cocoons doesn't include those in which the hosts died at the prepupal stage. Thus, each value of the parasitism reveals ordinarily the parasitic activity in the period between two consecutive census days. However, it must be taken into account that before spinning the cocoon, the moth spends 2～3 days in the prepupal stage, which is fairly vulnerable to attack by the fly. This table shows that the fly actively attacked the host cocoon from mid-July to mid-August, indicating that the adult fly existed in the field in this period.

It took at least 7 to 10 days in summer for the adult flies to emerge from the puparia after the fly larvae emerged from the host. Thus, it may be about July 20th at the earliest when the fly emerging from the host prepupae could begin to attack the host cocoons, even if the adult fly could lay eggs immediately after the emergence. Actually, most of the adult flies, whose larvae emerged from the host prepupae of which the larvae were collected on July 1st and 15th, 1973, emerged from their puparia in early August. The date of July 29th was the earliest for the adult fly to emerge. Therefore, the adult flies that attacked the host cocoons in the period between about July 10th and July 29th were presumably originated from individuals that emerged from other hosts than the pine moth.

According to IGARASHI (personal communication), the life span of the adult fly was about one month, and its maximum was only 12 days in the present experiment. Thus, the adult flies which emerged in May would almost die out by early July. Therefore, a considerable part of the adult flies that attacked the host cocoons in July would derive from individuals that emerged from other hosts.

1. Annual cycle of parasitism

The annual cycle of the parasitism to the pine moth by the fly is supposed to originate in spring during the period from late April to late May every year. This supposition is given to simplify the discussion about the host-parasite relationship between the pine moth and the fly. The existence of the other hosts in winter would not so greatly affect the basic relationship, because the fly didn't attack the moth larvae until May in spring.

On this supposition, it is deduced that the fly which parasitized the moth larvae from May to mid-June derived from the eggs laid by the adult fly originating from the spring emergence. And also, it is deduced that the adult fly deriving from spring emergence also attacked the other hosts, so that the adult fly of the next generation can attack the moth cocoon again in July.

From the supposition that the life span of the adult fly is as long as one month, it is inferred that the adult fly in October would derive from other hosts than the moth pupa, because the fly that emerged from the moth pupa by late August would die out in September. Presumably, the fly attacked the other hosts after its emergence from the moth pupae in August. It would be mid-October when the fly emerging from the 4th instar larvae of the moth began to attack the moth larvae.

It took only about 10 days for the fly larva to attain maturity in the host pupa and to emerge. So, it would take only about 20 days for the fly to reach the adult stage after it succeeded in parasitizing the host pupa. Thus, the emerging date of the adult fly would be early August if its egg was laid on the host cocoon in mid-July. The period of spinning the cocoon by the moth was about one month from mid-July to mid-August. Therefore, part of the flies emerging from the pupae by late July would be able to find the available host cocoons to attack.

On the basis of the survey and the discussion above, the annual cycle of the parasitism is schematically shown in Fig. 5. The diagram tentatively shows that the fly is able to complete its life cycle solely on the pine moth. The fly parasitizes the moth larva in September and overwinters in the host, and it emerges in the next spring. Thereafter the fly parasitizes the host larva by mid-June and emerges from the host prepupa. Again the fly attacks the host cocoon and emerges from the host pupa in August. Then the fly parasitizes the moth larvae of the next generation in September. A part of the fly population could be maintained every year in this manner.

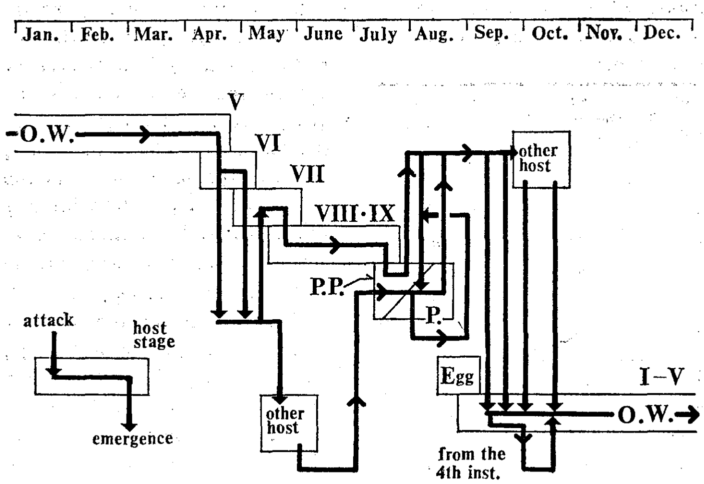

Fig. 5. Schematic diagram of the annual cycle of the parasitism to the pine moth by *C. bombylans*
P.: pupa, P.P.:prepupa, O.W.: overwintering

The fly population may be confronted with the shortage of host cocoons in summer if the fly depends solely on the pine moth to complete its life cycle. Most of the host larvae spin their cocoons in July (see Table 4), while most of the adult flies emerging from the host pupa begin to attack the host cocoons in early August, as discussed earlier. Many adult flies will not be able to find available host cocoons in August. The asynchrony in the period of spinning of the cocoon by the moth and the adult fly emergence will give low survival value to the fly, especially in those years when the host population density is low.

On the basis of the discussion above, it is inferred that after spring, hosts other than the moth are very important to cause such a high parasitism of the pupal stage of the pine moth as observed in 1973 (Table 2). It should be hosts other than the pine moth that produce the adult fly in late July when the available host cocoons are most abundant. Also, the other hosts may play an important role for the fly to maintain its population safely even if the fly would complete its life cycle mainly on the pine moth.

2. *Comparison of parasitism between localities*

IGARASHI (1972) reported that *C. bombylans* which overwintered in the larva of the pine moth emerged from the host larva in May, and thereafter the fly emerged again from the host during the cocoon-spinning period from early to mid-July at Misawa City, Aomori Pref. and Esashi City, Iwate Pref. He rarely observed the fly emergence from the host in autumn. According to KOKUBO (1964a, b, 1968), the fly passed the winter in the moth larva and emerged from the host from April to May at Chiba City, Chiba Pref. and in Kashima district, Ibaraki Pref. In Kashima, the fly killed the host ranging from the late larval stage to the pupal stage after spring, and it mostly emerged from the pupal stage. In 505 cases observed, 26 emerged from the prepupa and 479 from the pupa in 1963. At Chiba, the fly emerged from the host from mid-June to early July, mainly from the host pupa. IGARASHI didn't observe the fly emergence rom the host larva in autumn at Chiba.

The fly would parasitize the moth larva in autumn, overwinter in the host and complete the generation in the next spring in these localities as in Nagoya. But the host-parasite relationship in these localities seemed to be different from that in Nagoya after the spring emergence.

In these localities, the moth larva began to pupate earlier than in Nagoya. The moth larva began to pupate in late May in Kashima (KOKUBO, 1965), in mid-June at Chiba (KOKUBO, 1968) and in late June at Misawa and Esashi (IGARASHI, 1972). So, the adult fly deriving from spring emergence was able to survive to attack the host cocoon. It may have been difficult for the adult fly to lay eggs on the moth larvae because many moth larvae had already reached the final instar when the adult fly began to attack. The fact that most of the flies emerged from the host pupal stage after the spring emergence in these localities may indicate such circumstances that the fly attacked mainly the host cocoons.

On the other hand in Nagoya, the fly had two periods of attack after the spring emergence. The fly attacked the moth larva from May to mid-June (Table 1) and attacked the cocoons after mid-July (Table 1 and 2). Thus, it appears that the host-parasite relationship in these localities after the spring emergence is different from that in Nagoya.

This difference is caused by the different length of the host larval stage after spring. Therefore, it is concluded that there is some local variation in the annual life cycle of the parasitism by the tachinid fly, mainly depending on the life history of the moth which varies from north to south in Japan (HABU, 1968, 1976; KOBAYASHI, 1972).

KURANAGA (1975) surveyed the mortality of the pine moth covering seven generations in Kyushu district. In his survey, the fly emerged from the pupal stage every year and caused heavy mortality in some years. But the fly emergence from the host larva was observed only for one generation in Oura experimental station after overwintering, and was observed only for three generations in Kinposan experimental station before overwintering. Thus, in both sites, the fly should depend on some other hosts to complete its life cycle every year. Therefore, it is important to clarify the alternative hosts for a better understanding of the host-parasite relationship between the pine moth and the fly.

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