Seasonal Changes of the Proportions of Mated Females in
the Field Population of the Rice Leaf Roller,
Cnaphalocrocis medinalis GUENÉE
(Lepidoptera : Pyralidae)

Takashi WADA, Masahiro KOBAYASHI and Mitsuaki SHIMAZU¹

*Kyushu National Agricultural Experiment Station,
Chikugo, Fukuoka 833 Japan*

(Received August 21, 1979)

Observations were made of the mating, ovarian development and fat condition of the rice leaf roller, *Cnaphalocrocis medinalis* Guenée, collected from fields and by light trap in 1977 and 1978. It became clear that the proportions of the mated females fluctuated extremely by season. Most of the females collected in the paddy fields mated from June to early September. Thereafter, the proportions of mated females declined greatly up to mid-October, when almost all female moths contained immature ovaries and abundant fat body in their abdomens. From late October through the rest of the season the mated females, most of which looked lean, increased considerably in number. Some difference of the reproductive conditions was also noted among the three kinds of samples : female moths collected in the paddy fields, in the grassy fields and those captured by light trap. Some possible causes for the disappearance of the mated females in autumn are discussed.

INTRODUCTION

The rice leaf roller, *Cnaphalocrocis medinalis* GUENÉE, often causes economic loss to rice production in Kyushu, southwest of Japan by heavy infestations. Recent outbreaks occurred in 1973 and 1975. Some ecological aspects such as whether or not this species can overwinter in mainland, Japan, have been unsolved until now. In 1977, many moths were captured on a vessel in the East China Sea, a long distance from land (KISIMOTO, 1978) suggesting that this species may be a long-distance migrant.

The seasonal population trends of the pest in paddy fields have been studied since 1977. It was usually in mid-June when a few moths were first detected in a paddy field of the early planting culture. Then, the population level of the rice leaf roller gradually increased as the generations advanced until late August, but after mid-September although many moths were still inhabiting in the paddy field, the larval density decreased gradually (WADA and SHIMAZU, 1978) and very few eggs were found on the rice leaves (KOBAYASHI et al., unpublished). A remarkable reduction in proportion of mated females after early autumn was considered to be one of the

¹ Present address : Forest Experiment Station, Inashiki-gun, Ibaragi 300-12, Japan.

reasons for this phenomenon.

Reported here are the results of investigations concerning the reproductive status of adult females, including copulation and ovulation of the adult moths in the paddy field and the grassy field.

MATERIALS AND METHODS

Adult moths used. Samples of adult females were classified into the following three groups: moths collected from the paddy fields, those collected from the grassy fields and samples caught by a light trap. The paddy field: several paddy fields in Kyushu National Agricultural Experiment Station were surveyed, some of which were early planting culture. The grassy field: most of the moths were collected at a levee of the Yabe River about 3 km away from the Experiment Station and a hollow place around a pond at an elevation of about 100 m on Kiyomizu Hill which is located about 6 km from the Station. The light trap: a light trap equipped with a 20 w chemical fluorescent lamp (Toshiba, FL20 BL) was operated in the paddy field at the Experiment Station.

The proportion of mated females. The proportions of mated females in the paddy field were estimated by the following procedure until September 22, 1977. Female moths collected from the paddy field were reared individually in small plastic cups 6 cm in diameter and 4 cm in depth in which a piece of moistened cotton was added to maintain high humidity. These cups were kept at 25°C under a long day condition in the laboratory. After two nights, the number of deposited eggs was recorded. The proportion of mated females in the field was estimated by the rate of moths which had deposited fertilized eggs. After September 26, female moths collected from the field were dissected under a binocular microscope to check the presence of the sper-

Fig. 1. Various developmental grades of the ovary of *C. medinalis*.

matophore in the bursa copularix. Similarly, moths caught by the light trap in 1977 and 1978 were dissected for examination.

Development of the ovary. On dissection, observations were made of the development of ovaries and the amount of fat body in their abdomens in 1978. Each ovary of a newly emerged female consisted of four pairs of ovarioles which contained oöcytes measuring at most about 0.1 mm in width. If the adult female is allowed to feed on sugar, yolk deposition within oöcytes will soon occur, and in a few days oöcytes will develop to mature eggs measuring about 0.3 mm in width. The ovaries were classified into 4 grades on the basis of the developmental stage (Fig. 1). Grade 1: the ovarioles are transparent and fine like a thread and oöcytes do not develop at all. These ovaries with a little yolk deposition and an enlargement of oöcytes, but with ovarioles not yet colored and appearing transparent or white under a microscope were included in grade 1. The width of the largest oöcyte is under 0.2 mm. Grade 2: oöcytes near the oviduct appear yellow by yolk deposition, but the ovaries have no mature eggs. The largest oöcyte is about 0.2 mm in width. Grade 3: mature eggs observed in the ovarioles with a mean number of mature eggs below 10 per ovariole. Grade 4: mature eggs with a mean number of mature eggs above 10 per ovariole.

RESULTS AND DISCUSSION

The proportions of mated females in the adult population of the paddy field

In 1977, about 60–80% of the female moths, which were sampled in the paddy fields from early August to early September, deposited fertilized eggs in the laboratory (Table 1). This result suggested that the population in the field at that time maintained the rate of mated females at a high level. Thereafter, from late September, the number of mated female decreased greatly.

Table 2 indicates the seasonal changes of the proportions of mated females in the paddy fields in 1978. Usually the first adults of this species tend to be detected in mid-June in the paddy field of the early planting culture in Chikugo. These moths are considered to be immigrants from somewhere because we did not find any infested

Table 1. THE PERCENTAGE OF MATED FEMALE MOTHS IN THE FIELD POPULATION IN 1977

Date	Place	No. of samples	No. of females			% of mated females
			Mated	Virgin	Deposited none	
Aug. 7	Paddy field	20	15	1	4	(75) ^a
10	"	26	15	1	10	(60)
Sept. 6	"	13	8	0	5	(67)
22	"	5	0	0		0
26	"	26	1	25		4
27	"	26	2	24		8
Oct. 1	Grassy field	49	0	49		0
13	Paddy field	21	1	20		5
26	"	10	0	10		0
Nov. 14	"	7	1	6		14

^a The percentage in parenthesis indicates the value estimated from the oviposition test.

Table 2. COPULATION AND OVARIAN DEVELOPMENT OF FEMALE MOTHS IN THE POPULATION OF THE PADDY FIELD IN 1978

Date	Culture	No. of females			% of mated females	Development of ovary					
		Dissected	Mated	Virgin		No. of females dissected	Grade				
							1	2	3	4	
June	14	Early	15	14	1	93.3	15	1	1	12	1
	17	"	33	32	1	97.0	31	0	1	7	23
July	1, 2	"	7	5	2	71.4	4	0	0	1	3
	11	"	9	0	9	0.0	9	2	7	0	0
	12	"	23	1	22	4.4	23	4	18	0	1
	15	"	18	2	16	11.1	18	3	8	3	4
	19	"	14	10	4	71.4	14	2	5	3	4
	27	Ordinary	10	7	3	70.0	10	0	3	3	4
	31	"	36	34	2	94.4	36	0	2	7	27
Aug.	4	"	15	15	0	100.0	15	0	0	9	6
	8	"	21	17	4	81.0	8	3	1	8	9
	12	"	31	20	11	64.5	31	1	8	6	16
	16	"	33	28	5	84.8	23	0	3	5	15
	23	"	42	28	14	66.7	41	1	9	10	21
	28	"	29	13	16	44.8	27	5	9	4	9
Sept.	5	"	31	18	13	58.1	27	8	1	10	8
	12	"	52	1	51	1.9	23	20	1	2	0
	20	"	44	3	41	6.8	42	38	1	3	0
	26	"	29	0	29	0.0	29	28	1	0	0
Oct.	4	"	35	1	34	2.8	35	33	0	2	0
	12	"	24	0	24	0.0	24	24	0	0	0
	17	"	39	0	39	0.0	39	38	0	1	0
	30	"	35	3	32	8.6	35	25	5	5	0
Nov.	8	"	40	17	23	42.5	40	15	12	13	0
	10	"	32	7	25	21.9	32	17	8	7	0
	16	"	31	7	24	22.6	31	11	10	10	0

leaves in the paddy fields and other fields before June. The immigration of the adults into the paddy field occurs a few times every year during June and July. The immigration was detected twice in 1978; the moths which were collected from June 14 to 17 and on July 1, 2 seemed to belong to the first and the second immigrants respectively. These immigrant populations showed high rates of mating; more than 90% in the first immigration and 71% in the second one. About half of the female moths collected on June 17 had more than two spermatophores.

The moths collected in mid-July, which seemed to be the new generation grown in the paddy field, showed low proportions of mated females at the beginning of adult emergence, i.e., July 11, 12 and 15, but on July 19, the late period of the emergence of the generation, the figure reached 71%. The occurrence of this new generation was observed only in the fields of the early planting culture, because the first immigrants had arrived before late June when fields of normal season culture were transplanted. Therefore, the population density of the new generation tended to depend greatly upon the time of transplanting in the paddy field. Owing to the density gradient, new adults which emerged in July in the field of the early planting culture are considered

to disperse to the field of the normal season culture in which the rice plants grow sufficiently for larval infestation. Consequently, the fact that the major portion of the samples collected from the early planted field were newly emerged moths resulted in low proportions of mated females on the first three surveys in mid-July.

After late July the moths were collected from the paddy field of the normal season culture. The proportions of mated females collected from late July to early September varied from 44 to 100%. Thereafter, the proportions decreased greatly to 1.9% in mid-September. This low level continued to late October, especially between September 26 and October 17, during which only one out of 127 females examined had mated. In November, the proportions of mated females increased again to more than 20%.

As usual in Chikugo, all the rice plants were harvested between late October and early November. Therefore, it was impossible to capture the moths in the paddy field after mid-November.

The proportions in the grassy field

After August in Kyushu, we often find numerous moths of the rice leaf roller at certain places, such as grassy fields on hills, levees of rivers, fallows and orchards, where many species of grass grow thick, and the population densities of moths at these places increase after late August. In late September the authors caught 71 moths by sweeping ten times with a net 35 cm in diameter at the survey site of the hollow located halfway up Kiyomizu Hill.

Physiological conditions and ecological behaviors of these moths in the grassy field were possibly different from those in the paddy field for the following reasons: 1) The moths were observed at fixed places every year and the densities were remarkably

Table 3. COPULATION AND OVARIAN DEVELOPMENT OF THE FEMALE MOTHS IN THE POPULATION OF THE GRASSY FIELD IN 1978

Date	Place	No. of females			% of mated females	Development of ovary				
						No. of Female dissected	Grade			
		Dissected	Mated	Virgin			1	2	3	4
Aug. 9	Levee	39	9	30	23.1	37	12	16	2	7
17	"	64	41	23	64.1	50	1	17	12	20
23	"	25	3	22	12.0	18	5	10	3	0
Sept. 7	Hill	52	16	36	30.8	33	12	9	8	4
13	"	39	15	24	38.5	39	17	7	12	3
20	"	32	3	29	9.4	32	24	4	3	1
26	"	48	1	47	2.1	36	33	3	0	0
Oct. 3	"	37	0	37	0.0	30	30	0	0	0
12	"	12	0	12	0.0	12	12	0	0	0
12	Levee	9	1	8	11.1	9	6	2	1	0
18	"	10	2	8	20.0	8	3	3	2	0
Nov. 5	"	26	3	23	11.5	26	15	7	4	0
9	"	28	4	24	14.3	28	3	18	7	0
9	Hill	38	3	35	7.9	38	26	10	2	0
16	Levee	33	14	19	42.4	33	8	9	16	0
22	Fallow	10	1	9	10.0	10	3	5	2	0

high compared with those in the paddy field. 2) Few eggs were found on the weeds nearby, notwithstanding the numerous moths on the weeds. 3) These moths were apparently immigrants coming from somewhere. Few stale infestations were found on weeds, which indicated that these adults had not emerged there.

In 1978 the rate of mating and ovarian development were investigated for the adults in the grassy fields (Table 3). The seasonal changes of the proportions of the mated females in the grassy fields showed nearly the same pattern as those in the paddy fields, namely, extremely low proportions of mated females from mid-September to mid-October and considerable increase in the proportion of mated females after late November. But there were some differences between populations. More mated females were caught in the paddy fields than in the grassy fields throughout August. Further, although 1.9% of samples were mated on September 12 in the paddy field, 38.5% were mated in the grassy field on September 13. This fact indicated that the critical time when mated females had suddenly disappeared was different between populations. Difference was also noted in the time when the proportion of mated females increased again being slightly earlier in the grassy field than in the other fields.

The moth density in the grassy field decreased gradually from mid-October. Then, after several frosts in mid- and late November, no moths were observed in the field. As previously mentioned, the moths in the grassy field seemed to be immigrants from somewhere, but the original sites of immigrants remains unknown. The physiological and behavioral differences between the populations are not yet sufficiently studied.

Moths caught by the light trap

Figure 2 shows the mating status of the moths caught nightly by a black light trap in 1977 and 1978. In both years the number of mated females caught decreased remarkably from mid-September, which corresponded to the population in paddy and grassy fields. The mating characteristics of the females caught by the light trap seemed to parallel closely those of females in the field. But there were a few differences in detail especially in 1978. First, many virgin females were caught by the light trap

Fig. 2. Mating status of female moths caught by the blacklight trap.

in August when a high proportion of the mated females was observed in the paddy field. Secondly, at the beginning of mid-September more than half of the females caught by the light trap were mated in spite of the fact that only 1.9% of females collected from the paddy field on September 12 contained one spermatophore. From these facts, the mating status of the females caught by the light trap resemble those of the population in the grassy field.

Development of ovary

Yolk deposition and enlargement of oöcytes were observed in the ovaries of all the mated females examined. This suggests that egg maturation and its production are likely under hormonal control triggered by copulation as with some lepidopterous insects (WIGGLESWORTH, 1950). For this reason, the higher the proportion of mated females, the more females tended to have mature eggs in their ovaries (Grade 3 or 4).

Generally, more than half of the mated females collected from the paddy field from June to early September had over 10 mature eggs per ovariole (Grade 4), while most of the virgin females had rather large oöcytes, but not fully developed yet (Grade 2). Contrarily, most of the virgin females collected from mid-September to mid-October, when mated females were rarely observed, had immature ovaries and an abundance of fat body (Grade 1). Such moths appeared to be newly emerged adults, judging from the conditions of ovaries and fat body.

The proportion of mated females went up again from late October but many of the moths looked somewhat lean and exhausted. Namely, the mated females, the ovaries of which were all grade 3 had poor fat body in this season. Changes were also observed in reproductive conditions of the virgin females. Individuals containing the ovaries of grade 2 increased in number instead of grade 1, but they differed in poor fat body from the virgin females in July and August.

Some speculations on the disappearance of mated females

Since the results of surveys conducted for two years showed a very similar tendency, the proportions of mated females in the field population seemed to fluctuate much seasonally every year in Chikugo. Three distinct phases according to the ovarian development, amount of fat body and the status of mating could be categorized. The first phase was June to early September when most female moths were mated in the paddy field. The second phase, from mid-September to mid-October, was characterized by the disappearance of mated females and the appearance of fatty moths. During the third phase from late October through the rest of the season proportions of mated females increased again and the status of ovaries was somewhat different from those in the preceding two phases. Still more, almost all the moths look lean in this phase.

Although the cause for the sudden disappearance of mated females in early autumn is still obscure, we may suggest some possible hypotheses to explain these phenomena. A lack of such essential factors for mating as temperature, food or some unknown ones may be considered. Otherwise, unknown factors may harm the copulation of this species. In fact, a high temperature is known to bring about injurious effects on mating in some insects, for example, *Bombix mori* (KATSUNO, 1977). Any impediment by high temperature is not expected in the case of this moth, because extreme decrease of the proportions of mated females occurred from early autumn. On the mating behavior

of the rice leaf roller, the lower limit of temperature has not been reported, but it is unlikely that only the action of low temperatures at night prevents moths from copulation for the following reasons. First, after late October mated females considerably increased in number in the field. Second, the night temperature in mid-September was much the same as that in mid-June when most of the female moths collected were mated. Third, the critical period of the disappearance of mated females was slightly different between the populations in the paddy field and the grassy field.

It is well known that some species of insects have to feed on certain nutriment in the adult stage to complete normal reproduction. In the case of the female rice leaf roller having immature ovary on emergence, her ovarian maturation was accelerated by feeding on sugar. Still more, the proportion of mated females was remarkably high when the moths were reared on sucrose solution compared with water in the laboratory (WADA, unpublished). Almost no virgin females collected in autumn had developed ovaries, though their ovaries develop soon when fed on sucrose. Thus, the disappearance of mated females in autumn might be caused by a lack of some nutriment essential for mating.

Another hypothesis is concerned with the reproductive diapause. The diapause of the adult stage is generally characterized by arrested development of the ovary. In the majority of the cases, the moths during hibernation or aestivation are unmated and fatty as exemplified by the bogong moth, *Agrotis intusa* (COMMON, 1954). SATO and KISHINO (1978) reported that in the immature stage of the rice leaf roller, diapause had not been induced by various combinations of light and temperature, but they did not refer to the adult diapause. At first glance, moths collected in the grassy field look like the hibernating population. But, all of them disappeared after several frosts. Apart from overwintering of this insect in the adult stage, the mating behavior and the development of the ovary might be arrested by some environmental factors.

Lastly, there is a possibility of a phenomenon incidental to the migration or the dispersal. Many studies on insect migration by flight indicated that migration by females of a wide range of species often occurs during sexual immaturity of the imago (JOHNSON, 1969). The female migrants are usually virgin and have immature ovaries. An aspect of a long-distance migrant of the rice leaf roller has been clarified as described previously, and the moths collected from the paddy field before early July and the ones collected from the grassy field seemed to be immigrants, setting aside the distance. The virgin females collected from the paddy field after mid-September may be in the teneral stage before dispersal from the paddy field where they developed. Similar tendencies concerning the mating status, i.e., the proportions of mated females fluctuated greatly by season and crop in which moths were captured, have been reported in *Heliothis zea* (CALLAHAN, 1958; LOPEZ et al., 1978), *H. virescens* (STADELBACHER and PRIMMER, 1973) and *H. armigera* (ROOME, 1975), although more mated females tended to be found compared with the rice leaf roller. Concerning the disappearance of mated females in *Heliothis*, STADELBACHER et al. (1972) suggested that the decline in mating activity could have been caused by high temperature, but LOPEZ et al. (1978) reported that mass dispersal from the mature and unattracted crop could be regarded as the major cause of these phenomena. Special attention should be given to the similarity of the mating status between the rice leaf roller and *Heliothis* species, though most of the surveys of *Heliothis* are based on moths caught only by light traps. Early September, when the proportions of mated females of the rice leaf roller began to de-

crease, seems to be a turning point of the nutritive condition of the rice plant which, then, starts heading. Concerning this nutritive condition for the larvae, WADA (1979) indicated that the rice plant after late August is not considered a favorable host plant for the larva of the moth. It is possible that this species will change its habitat on account of worsening environmental conditions including the host plant.

ACKNOWLEDGEMENTS

The authors wish to express their thanks to Dr. T. YUSHIMA and Mr. Y. MIYAHARA of Kyushu Agricultural Experiment Station, for their critical reading of the manuscript. Thanks are also due to Mr. S. HIGASHI for his much help in collecting insects.

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