

Synchronous flashing in the Japanese firefly, *Luciola cruciata* (Coleoptera: Lampyridae)

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ゲンジボタルの同時明滅

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東南アジア一帯に分布する *Luciola* や *Pteroptyx* 属ホタルは特定の木に多数の個体が止まり、一斉に明滅（同時明滅）することが知られている。この特異な習性は雄にのみみられ、配偶行動に重要な役割を果たしているものとされている。同様な習性が日本のゲンジボタル *Luciola cruciata* にも認められるが、群飛しながら同時明滅する点で他種と異なる。飛翔中のホタルの発光パターン解析は技術的にきわめて困難であったことから、ゲンジボタルの同時明滅について神田（1935）、OHBA（1983）が報告しているのみで不明な点が多かった。そこで筆者は高感度TVカメラや光増幅装置などを駆使した全く独自の方法により群飛するゲンジボタルの同時明滅の発光パターン解析や行動学的意義などについて検討を加えた。

ゲンジボタルは日没後に群飛しながら30~40分間、一斉に明滅を繰り返す。群飛する個体はほとんど雄であり、雌は葉や茎にとまり時々不規則に発光する。同時明滅の発光間隔は2秒前後（短周期型）と4秒前後（長周期型）の2型が認められた。今回の観察では中部地方以西の個体群は全て短周期型であったことから両型は棲み分けている可能性が高い。ゲンジボタルの同時明滅は雄にのみみられる習性であり、葉上で不規則な光を放つ雌を効率よく探すように適応した雄の行動と考えられる。短周期型と長周期型の分布状況、また両型が遺伝的に固定されたものか否かなどについて更に研究の余地がある。

Introduction

Numerous observers have marveled at the beauty of the synchronous flashing in firefly. This interesting phenomenon is observed in several tropical countries, stretching from India to New Guinea, and particularly in Thailand, Burma and Malaya (HARVEY, 1952; MORSE, 1916; REINKING, 1921; MORRISON, 1929; SMITH, 1935; HANEDA, 1966; 1941; BUCK and BUCK, 1966; 1968; LLOYD, 1972; 1973a; 1973b; HANSON, *et al.*, 1971; BUCK, *et al.*, 1981). In this phenomenon, the fireflies gather in trees in dense swarms and the males flash on and off rhythmically and synchrony. Thousands of individuals sometimes flash exactly together cycle after cycle (BUCK and CASE, 1961; BASSOT and POLUNIN, 1967). Many observers also have seen the beauty of synchronous flashing in flying individuals of the Japanese firefly, *Luciola cruciata* (e.g. KANDA, 1935). This species is the most famous Japanese firefly. Flash communication in Japanese fire-

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flies has been studied (OHBA, 1983), but the role of the synchronous flashing remained unclear. *L. cruciata* has a very peculiar mating behavior. Though many observers have tried to record and analyze the flash patterns of the flying males (e.g. YAJIMA, 1978; OHBA, 1979; 1983). However, the results are not satisfactory. In this paper, new methods of recording and analyzing flash patterns of flying fireflies are described and the synchronous flashing in *L. cruciata* is discussed.

Materials and methods

Observations and measurements of flash patterns are carried out at five localities in Japan (Fig. 1; Pl. 8). Flash patterns of flying fireflies were rec-

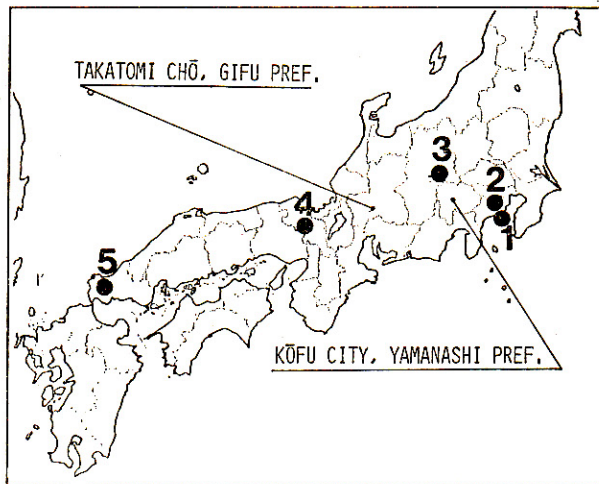


Fig. 1. Map showing localities of this work.

1. Nobi, Yokosuka City, Kanagawa Pref., 2. Ôike Park, Yokohama City, Kanagawa Pref., 3. Tatsuno chō, Nagano Pref., 4. Kiyotaki Riv., Kyoto Pref., 5. Era Riv., Toyoda-chō, Yamaguchi Pref.

ordred and analyzed as follows: Flash of fireflies were detected by an image-intensifire tube connected with a TV camera and the signals were recorded by a video tape recorder (VTR). The temperature rang during observations was 18–24°C. The TV camera used in this study was equipped with a CCD TV camera. There is no afterimage in flash recordings made by this method (Fig. 2. A). Measurements and analyzing procedure were as follow: 1) Flashes recorded on the VTR tape were displayed on a monitor TV (Fig. 2. B. 2) The flashes on the screen of the monitor were traced by a photomultiplier tube to be fed to a chart recorder. 3) Flash intervals and duration were read directly on the chart.

Study area Investigations of natural populations of fireflies were carried out at five localities. (1) Nobi, Yokosuka City, Kanagawa Pref., 35°13'N

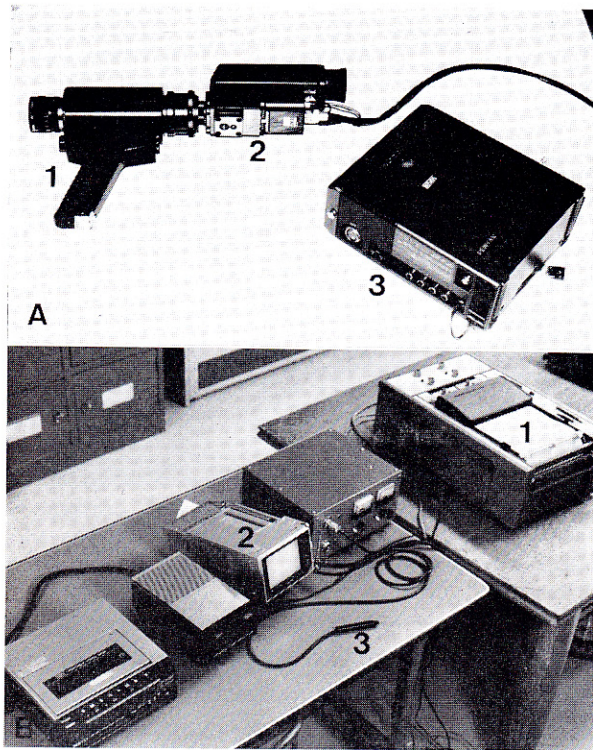


Fig. 2. Recording and analyzing apparatus of flash patterns of *L. cruciata*. A.1. Noctovision, A.2. TV camera, A.3. VTR. B.1. Penrecorder, B.2. Monitor TV., B.3. Photo sensor.

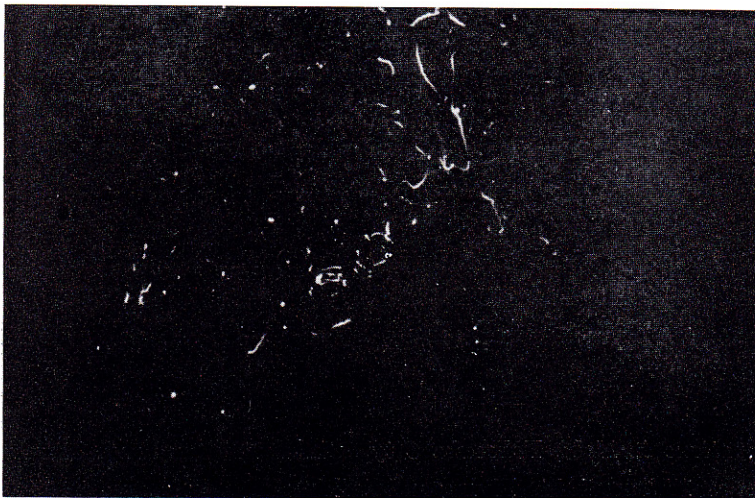


Fig. 3. Luminescence of synchronous flashing in *L. cruciata*. Exposure was 10 seconds on Kodak recording film, developed at ASA 200. Recording in Ôike Park, Yokohama City.



Fig. 4. Luminescence of synchronous flashing in *L. cruciata* in Era Riv., Toyoda-chô, Yamaguchi Pref., at 20°C. Exposure was 10 seconds on Kodak recording film, developed at ASA 200.

and 139°42'E. The fireflies emerge from a small stream at the foot of a hill. The stream has been used as an irrigation channel which is 60–120 cm in width and 5–20 cm in depth. The firefly habitat extends approximately 200 m long. (2) Ôike Park, Yokohama City, Kanagawa Pref., 35°27'N, 139°32'E. The fireflies emerge from a small stream that had been used as an irrigation channel. Recently, this area was graded to make a marsh and has been protected for the park of Yokohama City. Therefore, the area should remain in a favorable condition for fireflies. The stream runs along the marsh and in the folds of the hill, and is 60–200 cm in width and 1–10 cm in depth. It is bordered by trees and grass. There is little influence of artificial light near this area. (3) Tatsuno-chô, Nagano Pref., 35°59'N, 137°57'E. The fireflies emerge from a small artificial stream which is approximately 100 cm wide and 10–20 cm deep. The stream is bordered by grass and small planted trees. (4) Kiyotaki Riv., Kyoto Pref., 35°03'E and 135°40'E. The river runs in the folds of the hill. The river is 10–20 m wide and 10–100 cm deep, and bordered by hotels. (5) Era Riv., Toyoda-chô, Yamaguchi Pref., 34°12'N and 131°05'E. The river is 2–5 m wide and 5–50 cm deep. The fireflies appear for a distance of approximately 2000 m along the river.

Results

Observations in Nobi, Yokosuka City Observation and measurements were carried out on 15 June 1984. Flying and flashing activity began at 19:30. About two hundred individuals appeared along the small stream (Pl. 8). The peak flying activity was at 19:55. Thereafter, the flying activity gradually decreased. Flashing males approached to females and perched near them. Then their flash

Table 1. Flash patterns of synchronous flashing in *L. cruciata*.

LOCALITY AND DATE OF OBSERVATION	TIME	TEMP. (°C)	MALE NUMBERS	\bar{X}	SD	RECORDED VALUE (SEC.)
ERA RIV., TOYODA CHŌ, YAMAGUCHI PREF. 25 JUNE 1984	20:14	21.0	20 - 30	1.89	0.15	1.95 1.70 1.95 1.80 1.85 1.70 1.80 1.85 1.70 1.80 1.85 1.70 1.80
						2.10 2.10 2.00 2.10
	1	1.81	0.08	1.81	0.08	1.81 1.81 1.70 1.85 1.80 1.80 1.90 1.85 1.80 1.80 1.85 1.80 1.60
						1.80 1.80 1.95
	1	1.82	0.12	1.82	0.12	1.90 1.90 1.90 1.90 1.90 1.75 1.80 1.80 1.80 1.80 1.80 1.75
						1.50 2.00
	1	1.72	0.16	1.72	0.16	1.65 1.60 1.65 1.90 1.65 1.25 1.90 1.90 1.90 1.85 1.70 1.95 1.70
						1.80 1.70 1.80 1.70 1.70
	10 - 20	1.74	0.09	1.74	0.09	1.86 1.65 1.65 1.50 1.80 1.80 1.65 1.80 1.65 1.90 1.80 1.70
						1.75 1.75 1.75 1.75 1.75
21:30	21.0	1.72	1	1.72	0.13	1.95 1.70 1.85 1.85 1.55 1.80 1.45 1.70 1.70 1.70
						1.55 1.85 1.70 1.70
KIYOTAKI RIV., KYOTO PREF. 26 JUNE 1983	20:10	20.0	5 - 6	1.97	0.10	2.00 1.80 1.90 2.00 2.00 2.00 2.00 2.10 2.00 2.10
						1.98 0.11 2.10 1.80 1.80 2.00 2.00 2.00 2.00 2.00 1.90 2.10 2.10
TATSUNO CHŌ, NAGANO PREF. 3 JULY 1983	20:20	21.0	5 - 8	2.08	0.08	2.20 2.00 2.00 2.20 2.00 2.15 2.10 2.20 2.00 2.20
						2.10 2.20 2.00 2.10 2.00
	4 - 6	2.13	0.22	2.13	0.22	1.80 2.25 2.10 2.05 2.10 2.15 2.40 2.00 2.10 2.60
						2.40 1.75 2.10 1.85 2.10
20:40	21.0	2.13	1	2.13	0.30	2.00 2.40 1.80 2.00 2.50 2.35 2.10 1.85 2.85 2.00
						2.20 2.20 1.70 2.40 1.80
ŌIKE PARK, YOKOHAMA CITY, KANAGAWA PREF. 18 June 1984	20:00	22.0	7 - 10	4.28	0.27	4.60 4.15 4.40 3.90 4.10 4.10 4.45 4.50 4.70 3.90
						3.90 4.10 3.99 4.05 4.80 4.30 4.20 3.95 4.25 4.35
	1	4.18	0.24	4.18	0.24	4.35 3.95
						4.00 4.55 3.65 4.10 4.40 5.00
1	4.28	0.43	4.28	0.43	4.00 4.55 3.65 4.10 4.40 5.00	
					3.85 3.90 4.15 4.15 4.70 4.05 4.10	
1	4.13	0.26	4.13	0.26	4.35 4.10 4.30 4.50 4.50	
					4.70 3.40 3.70 4.30 4.10 4.65 3.80	
1	4.09	0.45	4.09	0.45	4.70 3.40 3.70 4.30 4.10 4.65 3.80	
					4.40 0.30 4.70 4.60 3.90 4.60 4.20	
20:00	23.0	4.05	5 - 6	4.05	0.56	4.40 4.00 3.40 3.50 4.40 4.20 3.80 3.90 4.55 4.60
						4.60 4.60 2.60 4.70 4.00 3.70 3.35 4.60
NOBI, YOKOSUKA CITY, KANAGAWA PREF. 15 JUNE 1984	20:00	23.0	5 - 6	4.05	0.56	4.40 4.00 3.40 3.50 4.40 4.20 3.80 3.90 4.55 4.60
						4.60 4.60 2.60 4.70 4.00 3.70 3.35 4.60

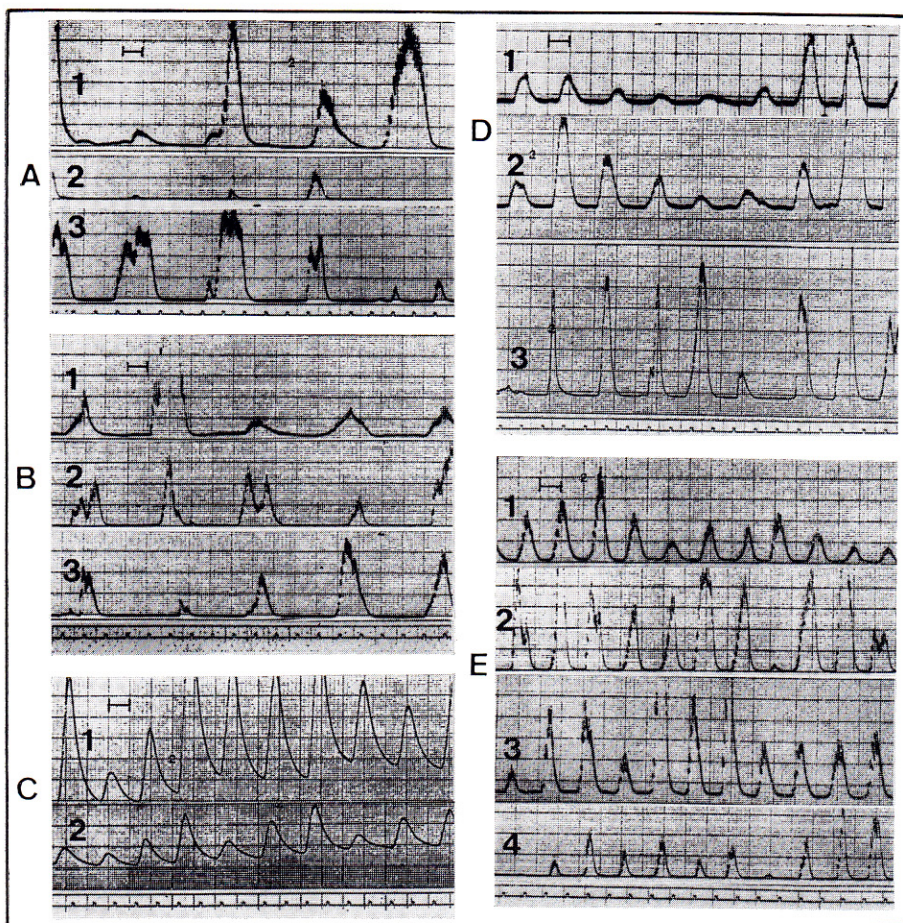


Fig. 5. Synchronous flashing in *L. cruciata*.

Flash rate of all the males is exactly synchronized. If a lag of timing is caused, they correct their flash rate with the next flashing.

Read left to right, Ordinate: relative intensity, Abscissa: time, scale indicating 1 second.

A.1-3. Recording in Nobi, Yokosuka City, Kanagawa Pref., at 23°C.

B.1-3. Recorded Ôike Park, Yokohama City, Kanagawa Pref., at 22°C,

C.1-2. Recorded in Kiyotaki, Kyoto Pref., at 20°C. D.1-3. Recorded in

Tatsuno-chô, Nagano Pref., at 21°C. E.1-4. Recorded in Toyoda-chô,

Yamaguchi Pref., at 21°C.

A.1,3, B.1-2, C.1, D.1-2, E.1,3, Flash pattern of five to six male in-

dividuals. A.2, B.3, C.2, D.3, E.2,4, Flash pattern of single male.

patterns became irregular. Synchronous flashing of male *Luciola cruciata* was observed only when they were flying. The intervals of their flash patterns were 4 seconds at 22°C (Fig. 5; Table 1). The frequency of flashes remains constant at 15 flashes per minute. Single male's individuals were approximately 4 seconds in interval (Table 1). Another species of firefly, *Luciola lateralis*, appeared

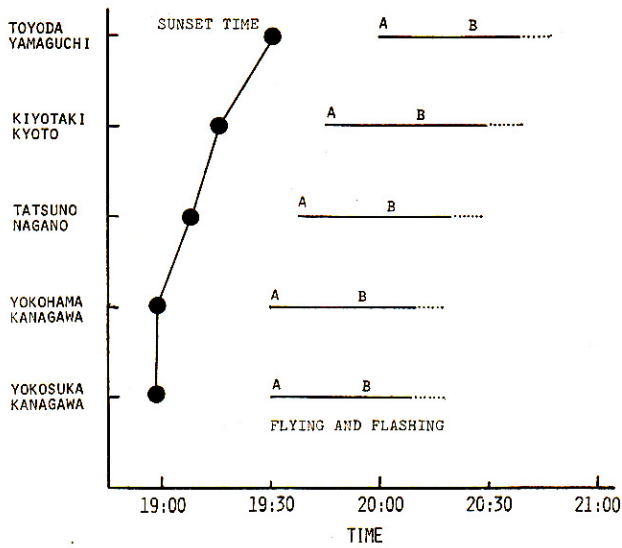


Fig. 6. Activity time of synchronous flashing in *L. cruciata* at five localities in Japan. A indicates males begin flashing, B indicates peak activity of synchronous flashing.

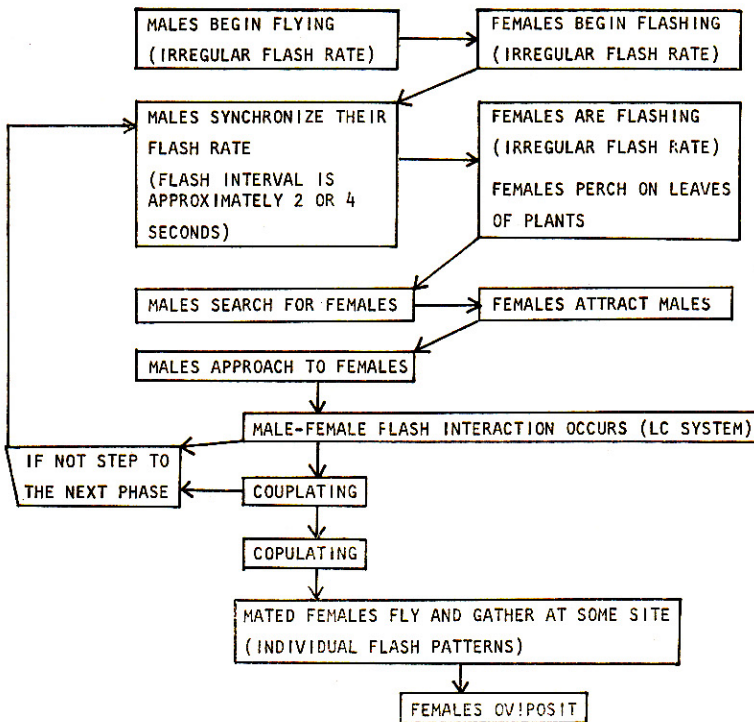


Fig. 7. Mating behavior in *L. cruciata*.

at the same site, but their flash interaction was not observed.

Observations in Oike Park, Yokohama City Observations and measurements were carried out on 18 June 1984. Flying and flashing activity began at 19:30. Five to six hundred individuals appeared along the small stream (Fig. 3), and they never flew away from the stream. The peak flying activity of this population occurred at 19:55. The flash patterns became very rhythmical. The flash were approximately 4 seconds in interval and 1 second in duration (Fig. 5; Table 1). After the synchronous flashing activity, the males approached to females or perched on leaves of plants. Thereafter, the flying activity gradually decreased (Fig. 6). They occasionally emitted irregular flashes.

Observations in Tatsuno-chô, Nagano Pref. Observations and measurements were carried out on 3-6 July 1983. Flying and flashing activity began at 19:38. The peak of flying and flashing activity occurred at 20:02 (Fig. 6), then one to three thousands individuals synchronized their flash rate. This phenomenon could be seen at a distance of approximately 100 meters. The females did not fly, nor synchronized their flashes. Flash patterns of males while synchronizing were approximately 2 seconds in interval and 1.0 second in duration at 21.0°C (Fig. 5, Table 1). The synchronous flashing activity ended at 20:40, and thereafter their flash rate became gradually irregular.

Observations in Kiyotaki Riv., Kyoto Observations and measurements were carried out on 26 June 1983. The fireflies began flying and flashing at 19:45 and the peak activity was reached at 20:15. After that they occasionally flew and flashes until daybreak. However, most males perched on leaves of trees or grass at 0:00, when mated females began flying. The flash patterns were approximately 2.0 seconds in interval at 20.0°C (Fig. 5, Table 1). Fifty to one-hundred individuals synchronized their flashing. Females did not fly and emitted irregular flashes. When a male detected a female's flashes, he approached to her. Thereafter, the male-female flash interaction occurred. Flying and flashing males were observed along the river for a distance of 3000 meters.

Observations in Era Riv., Yamaguchi Pref. Observations and measurements were carried out on 25 June 1984. The fireflies began flying and flashing at 20:14 and the peak activity occurred at 20:25. Two or three thousands of individuals appeared along the river (Fig. 4). The flash patterns were very rhythmical. The flashes were approximately 1.8 seconds in interval (Fig. 5, Table 1). Thereafter, the flying activity gradually decreased and their flash became gradually irregular.

Discussion

Some difference in the manner of synchronous flashing is noticed between *Luciola cruciata* and Southeast Asian fireflies, *Pteroptyx cribellata*, etc. In *L.*

cruciata, many flying males synchronously flash when they search for females. *P. cribellata* and other species of synchronously flashing fireflies gather in trees in dense swarms and it is the perched males that synchronize their flashes (MORRISON, 1929; HANEDA, 1966). Accumulated evidence indicated that the synchronous flashing behavior plays an important role in mating. This point should be further studied in detail. From my observations on *L. cruciata*, the flashing of males occurs periodically, when the flash interval is approximately 2 or 4 seconds. Two main types of flashes have been observed (KANEDA, 1935). One is slow rhythm flashing with a frequency of 16 flashes per minute. This type was observed in Kôfu City, Yamanashi Pref. The other type is fast rhythm flashing with a frequency of 30 flashes per minutes. This type was observed in Takatomi-chô, Gifu Pref. The two types are observed during this study also. The fast rhythm flashing populations appear in the western part of the Chubu District. This fact arouses our special interest. It should be consider from a wider viewpoint.

In the case of *L. cruciata*, synchronous flashing occurs only when males are flying, unlike other synchronous fireflies which synchronize their flash rate when they gather and perch on a tree (BUCK *et al.*, 1968; REIKING, 1921; HANEDA, 1966). In *L. cruciata*, the flash patern of perched male is similar to that of perched female, but they need to search for and recognize a potential mate. When males synchronize their flash, irregular flashes of perched females are suitable for the males to recognize and locate the females. It is considered that their mating behavior proceeds in the following phases (Fig. 7). In the first phase, most of males fly and synchronize their flashes. Females do not fly and do not synchronize their flashes. They perch on leaves of trees or grass and emit irregular flashes. Males are able to recognize females by their flashes. In the second phase, males find females, approach to them and a male-female flash interaction occurs (OHBA, 1983). Then they copulate, after copulation the females gather at some site and oviposit. The females fly and search for an oviposition site from midnight to daybreak. Flash communication of this species was reported in a previous study (OHBA, 1983), where it was suggested that the communication system of *L. cruciata* is similar to the Complex system (LLOYD, 1973). OHBA calls this the LC system.

L. cruciata emits flashes after sunset. The activity time is not the same at the five localities in Japan (Fig. 6), for example, in Nobi, Yokosuka City, synchronous flashing begins at 19:30, but at 20:00 in Toyoda-chô, Yamaguchi Pref. This fact indicates that the activity time is decided by the ambient luminosity.

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1. Nobi, Yokosuka City, Kanagawa Pref.



2. Tatsuno-chô, Nagano Pref.



3. Kiyotaki Riv., Kyoto Pref.



4. Era Riv., Toyoda-chô, Yamaguchi Pref.