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Flash Communication Systems of Japanese Fireflies[1]

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SYNOPSIS. Japanese fireflies range from nocturnal luminescent species to diurnal non-luminescent species. Their communication systems are classified into 6 types based on the following criteria: 1) Female responds to male's flashes after a fixed delay; 2) Male is directly attracted by female's light signal, the male perches on a leaf near the female, then the male changes his flashes with twinkling, and copulation behavior is released. However, the female may not respond to the male; 3) Male seeks female calling signal during the male's flying and synchronous flashing, then the male approaches the female, emitting flashes with various patterns, displaying walking-luminescing, sedentary signaling, chasing, and copulating; 4) Male is attracted by continuous luminescent signals of the female, and male perches near the female, then the male distinguishes the female's light organs shape. Thereafter, the male copulation behavior is released by her sex pheromone; 5) Male and female flight occurs in the daytime; when the male approaches the female, copulation is released by the female's pheromone; weak luminescent signals may be fulfilling the function of supplementary communication signals; 6) Luminescent signals have nothing to do with communication between male and female, and copulation is released by a sex pheromone.

INTRODUCTION

Most communication systems in luminescent fireflies have been studied in nocturnal species (*e.g.,* Buck, 1937; Buck and Buck, 1966, 1972; Lloyd, 1966); little is known concerning communication in crepuscular and diurnal species. About 2,000 species of fireflies are known throughout the world that have various kinds of communication systems.

Communication systems have been studied in 45 species of Japanese fireflies including one species of Rhagophthalmidae. Typical species are shown in Figure 1. The biology, including sexual communication and the ecology of diurnally active species, is poorly understood.

The purpose of this study is to establish a foundation of general knowledge concerning sexual communication of Japanese fireflies and to elucidate the relationship between morphology and behavior.

Based on my study (*e.g.,* Ohba, 1983*a*), the communication system of the Japanese fireflies is classified into 6 types (below) (Fig. 11).

COMMUNICATION SYSTEM OF *HOTARIA PARVULA*: HP SYSTEM (SYSTEM II)

In this system, the female responds to the male's flashes after a fixed delay (Ohba, 1980, 1983*a*, 2000). This system is known as System II in North American fireflies (Lloyd, 1971).The male is directly attracted by the female's light signal and copulation is induced. This female delay time is constant at approximately 0.24 seconds at 16°C (Fig. 2).

A coupled female never responds to male flashes and the female mates only one time. Therefore the female flash response serves not only to let the male know that ''I am here,'' but also to let him know that ''I have not coupled yet.'' When the male is not present near the female or the male has ceased flashing, the female begins to emit peculiar flashes as a calling signal. Thus, it is that the female flashes attract the male and bring about the male's flashing. If there are no males near the female, she continues to emit a calling signal.

Just before copulation, the female flash response interval gradually shortens. Finally, the flashes of both sexes are almost synchronized and they copulate.

The female flash response is induced by variable artificial flashes. If the interval is under 0.4 seconds, the female cannot respond to every flash. Female flash response is induced with male or artificial flashes (Ohba, 1983*a*).

There are two types of *H. parvula*. One is larger with body length 7–9 mm, the width of pronotum is greater than 2.1 mm and the flash interval of the flying male is 0.4–.09 seconds at 20–14°C. The other type is smaller with body length 5–7 mm, width of pronotum is smaller than 2.1 mm and the flash interval 0.2–0.5 seconds at 18–24°C. There are two flash patterns in each ecological type of *H. parvula*; One is fast, the other slow (Ohba, 2000). It is possible to distinguish their habitat, and background and the heredity of two ecological types by allozyme analysis (Suzuki *et al.*, 1993).

The smaller type is distributed from Hakone, Kanagawa Prefecture to the Ishikawa Prefecture.

In western Japan, the larger type is distributed at altitudes above 800 m, while the smaller type lives lower than 800 m altitude. I investigated flash communication in the smaller type at Tettacho, Okayama Prefecture, and compared it with the larger type flash communication reported by Ohba (1983*a*).

The smaller type flash rate is shorter than larger type when a male is flying and seeking a female.

When the male of larger type is placed together with

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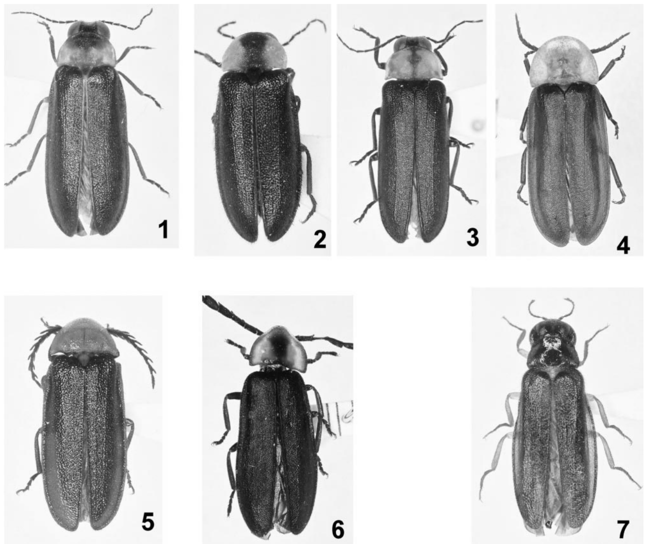

FIG. 1. Typical Japanese fireflies. 1. *Hotaria parvula*. 2. *Luciola lateralis*. 3. *L. cruciata*. 4. *Pyrocoelia rufa*. 5. *Cyphonocerus ruficollis*. 6. *Lucidina biplagiata*. 7. *Rhagophtalumus ohbai*.

the female of smaller type in the laboratory, they mate after their flash communication. If both types inhabit the same place in the field, they usually interbreed (Ohba, 2000). However, they are isolated by seasonal prevalence, altitude and habitat.

Flash patterns, structure of the compound eyes, antenna, and light organs are intimately involved in the communication systems of fireflies (Ohba, 1978, 2000).

The following species are classifiable as possessing an HP system based on field observations: *H. tsushimana* (Ohba, 1985), *Luciola yaeyamana*, and *L. kuroiwae* (Ohba, 1983*b*).

FLASH COMMUNICATION SYSTEM OF *LUCIOLA LATERALIS*: LL SYSTEM

When a flying male emits flashes (Fig. 3.1–3) and seeks a female's peculiar flashes (Fig. 4.1–3), it approaches the female to within 5–10 cm. The peculiar flash of the female plays an important role in attracting males (Ohba *et al.*, 2001).

In the next step, the male converts his flash pattern to single flashes with twinkling (Fig. 3.4–6). In the last step, both sexes continue to emit their peculiar flashes and thereafter they copulate.

Experimental results with male response flashes indicate that green, yellow, and red colored artificial flashes induce their copulation (Ohba, 1983*a*). Therefore the signal system is a simple type. No critical timing of the female response flashes is seen in this species (Fig. 4.4–6). They emit individual flashes and recognize each other.

L. lateralis. This species is widely distributed in Japan, Korea, and eastern Siberia.

I found that in the Hokkaido population, the rhythmic flashing period of the searching male is longer than 1 second and that individuals often take more than one year to reach maturity. However, in the other Japanese *L. lateralis*, the male interflash interval is about 0.5 seconds at 25°C (Fig. 3.1), and the life cycle is usually complete in one year (Ohba *et al.*, 2001).

In Korean individuals, the male flash interval is about 0.5 seconds at 22°C, as in the populations of Kyushu, Honshu, and Shikoku, but it often takes more than one year to reach adulthood (Ohba *et al.*, 2001).

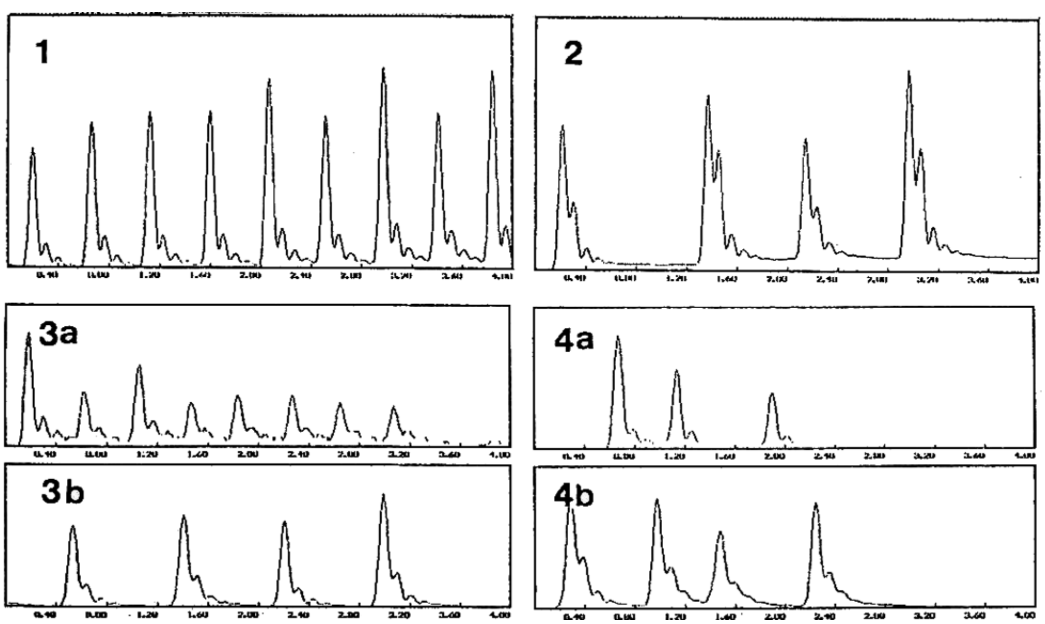

FIG. 2. Flash patterns and communication system of *Hotaria parvula* at Tettacho, Okayama Prefecture. 1. Flash pattern of male seeking a female. 2. Calling signal of a female. 3–4. Flash communication of a male and a female. 3a. Male flashes to female. 3b. Female response flashes to male males. 4a. Male flashes to female. 4b. Female response flashes to male flashes. Recording time: 4 seconds.

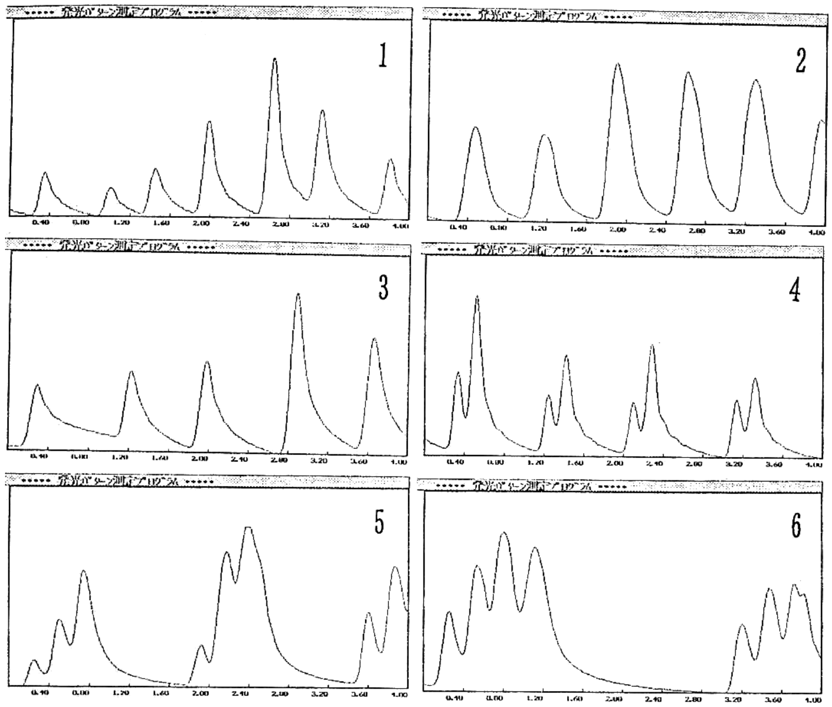

FIG. 3. Flash pattern of male *Luciola lateralis* flying and perching a short distance from a female. 1–3. Flying. 4–6. Perching (Ohba *et al.*, 2001). Recording time: 4 seconds.

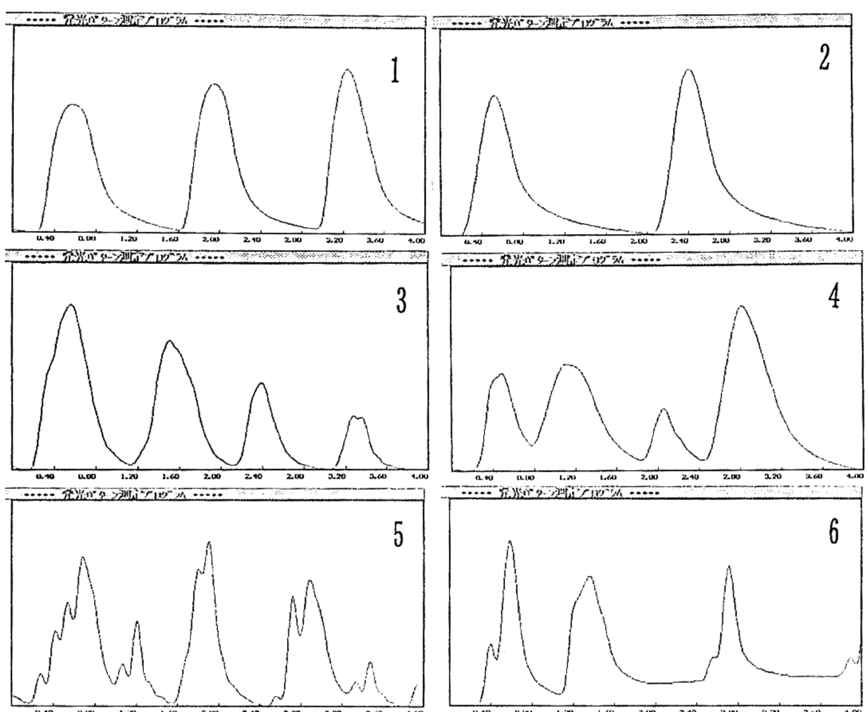

FIG. 4. Calling signals and communication system of *Luciola lateralis*. 1–2. Calling signal of *L. lateralis* in Bihoro, Hokkaido. 3. Calling signal of *L. lateralis* in Yokosuka City, Kanagawa Pref. 4. Flash communication of *L. lateralis* in Bihoro, Hokaido. Flash communication of *L. lateralis* in Yokosuka City, Kanaga Pref. 5. Flash communication of *L. lateralis* in Muju, Korea. Recording time: 4 seconds. In *L. lateralis*, the female does not respond to the male with a precisely timed flash (Ohba *et al.*, 2001).

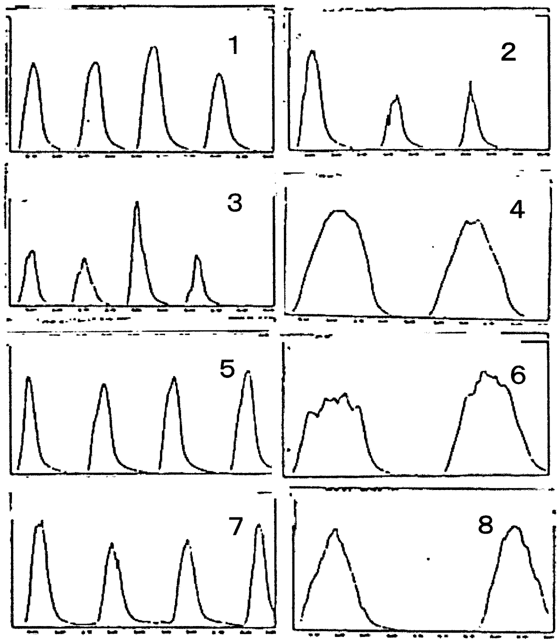

FIG. 5. Geographical variation of flash patterns in flying male *Luciola cruciata*. 1. Kitakyushu, Fukuoka Prefecture. 2. Toyodacho, Yamaguchi Prefecture. 3. Kiyotaki, Kyoto. 4. Tajimi City, Gifu Prefecture. 5. Nagaoka City, Niigata Prefecture. 6. Miura City, Kanagawa Prefecture. 7. Yuzamachi, Yamagata Prefecture. 8. Aomori City, Aomori Prefecture. Recording time: 4 seconds (Ohba, 2001).

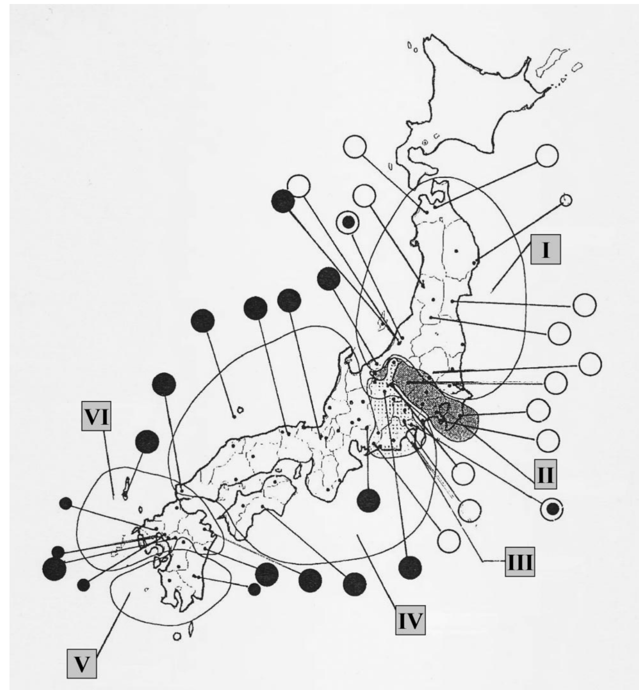

FIG. 6. Relationship of geographical variation of flash patterns in flying male *Luciola cruciata* and its 6 types of haplotypes based on mitochondrial DNA. I–VI. Clade of haplotype in *L. cruciata* (Suzuki *et al.*, 2002). Black circle: 2 second type, white circle: 4 seconds type, small black circle: 3 seconds type, double circle: 3 seconds type but flash duration is shorter than Kyushu's 3 seconds type (Ohba, 2001).

These results indicate that the Korean *L. lateralis* combines the characteristics of the population of Hokkaido, Honsu, Kyushu, and Shikoku.

Communication in this species is summarized in Figure 11. At the present, I think that Honshu, Hokkaido and Korean *L. lateralis* are the same species, but I am investigating their mitochondrial DNA.

The following species are classifiable as possessing an LL system based on field observations: *Curtos costipennis* and *C. okinawana* (Ohba, 1983*a*, 1986).

COMMUNICATION SYSTEM OF *LUCIOLA CRUCIATA*: LC SYSTEM (COMPLEX SYSTEM)

This system belongs to the Complex system (Lloyd, 1972) of the Papua New Guinea firefly, *L. obsoleta*.

The most famous Japanese firefly, the Genji-firefly, *Luciola cruciata*, is widely distributed in Japan with the exception of Hokkaido and Okinawa.

After sunset, the males begin to fly and flash slowly. Then they synchronize their flashes (Ohba, 1983*a*, 1984, 1986, 2001). The female does not synchronize her flashing to the males, but emits irregular flashes. Male and female flash patterns are similar.

When a male finds a female, it perches nearby and changes his flash patterns, as is the case of *L. obsoleta*.

A female response with fixed delay is not observed in *L. cruciata* (Ohba, 2001). The female's response does not always occur in sexual communication. The communication system of this species is as follows.

The female emits single pulsed flashes of light which are associated with the appearance of a flying flashing male. When the male finds a female, it approaches the female, which sometime responds to male flashes. Then, the male emits flashes with various flash patterns while approaching and walking near the female. Thereafter, they copulate. This flash communication system is similar to the complex system described previously by Lloyd (1971).

The flash patterns of *L. cruciata* are intermittent (Fig. 5). Such flashes are less suitable for critical timing of flash communication than those of *H. parvula*, but more suitable than *Pyrocoelia* fireflies which emit continuous light signals (Ohba, 1983*a*). However, the male *L. cruciata* find females because most males fly and synchronize while flashing while females do not fly and synchronize. Therefore, males can easily discriminate the female's light signal.

Communication in this species is summarized in Figure 11. I found that in the population of northern Japan, the rhythmic flashing period of the searching *L. cruciata* male is longer than in western Japan (Ohba, 1983*a*, 1984, 2001).

The individuals often take more than one year to reach maturity. However, in the western populations, the male interflash interval is about 2 seconds, and the life cycle is usually completed in more than one year. In northern populations, the male interflash interval is about 4 seconds (Fig. 6). Near the border area of distribution of both types, one more type of population

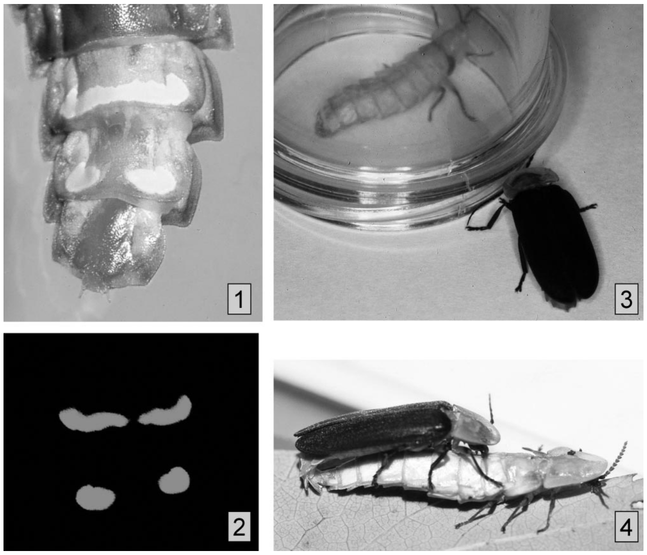

FIG. 7. Light organ of female and chemical communication of *Pyrocoelia rufa*. 1. External morphology of light organ in female. 2. Female light organ at night. 3. A male is attracted to a female by her pheromone. 4. A coupled male and female (Ohba, 1983*a*).

is recorded. There the male interflash interval is about 3 seconds (Fig. 6, small black circle).

Yamaga City, Kumamoto Prefecture and Chikugo City, Fukoka Prefecture, Kyushu, similar types of 3 second responders have been recorded (Fig. 6), that are better synchronized than the 3 second population of the border area of central Japan (Ohba, 2001).

Based on a morphological study in each population, I could not clearly distinguish a relationship between flash pattern and external morphology, except that the 4 second type occasionally lack a black marking in the pronotum.

Six clades of haplotype (based on mitochondrial DNA) have been found (Suzuki *et al.*, 2002), that can be related to flash patterns and behavior (Ohba, 2001).

Other species with an LC system, based on field observations include *Luciola owadai*, in which the male repeats its flashing periodically, and certain species in Southeast Asia, where great numbers gather in certain trees and flash in apparent synchrony (Buck and Buck, 1966; Case, 1980; Haneda, 1966; Hanson *et al.*, 1971; Lloyd, 1972).

Recently, Copeland and Mois (2003) reported a synchronous firefly, *Photuris frontalis* in North America.

THE COMMUNICATION SYSTEM OF *PYROCOELIA RUFA*: PR SYSTEM (SYSTEM I)

Males and females of *Pyrocoelia rufa* are indistinguishable in their luminescent patterns. The female is wingless and can only walk on the ground.

She emits a continuous light similar to that of the male and larva. The male may be recognized by the form and size of the light organ, which differs from that of the female (Fig. 7.1–2). It is impossible to send signals with critical timing using continuous light, which simply conveys position.

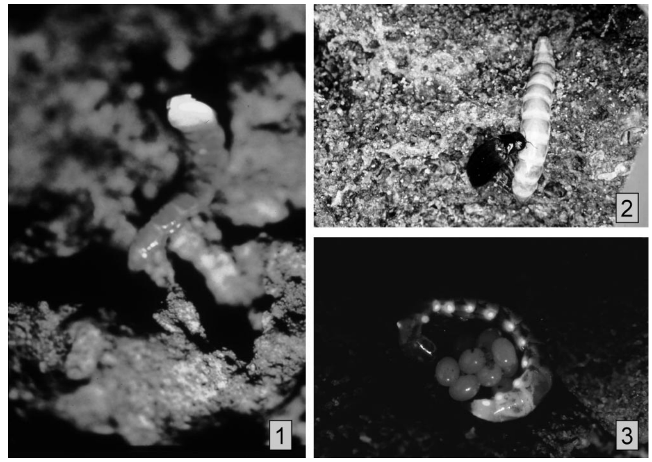

FIG. 8. Mating and defensive behavior of *Rhagophthalmus ohbai*. 1. Female extends her abdomen and emits a continuous light from the apex of the abdomen. 2. A male approaches a female and then attempts to copulate. 3. After copulation, the female lays eggs and holds them against her body and emits weak light from each body segment (Wittmer and Ohba, 1994).

The female attracts males using its continuous light, and it is presumed that sex pheromones participate as well (Fig. 7.3–4). Communication in this species, summarized in Figure 11, corresponds to System I of Lloyd (1971).

I think that this system may be seen as the ancestral system. The following species also have a PR system based on field observation: *P. atripennis* and *P. miyako* (Ohba, 1983*a*).

THE COMMUNICATION SYSTEM OF *RHAGOPHTHALMUS OHBAI*: MODIFIED PR SYSTEM

Adults of *R. ohbai* appear for two to three weeks in winter. At 18:30, females begin to emit continuous light from the terminal abdominal segments (Fig. 8.1,2). After mating, the female ceases light emission and oviposits and continues to hold her body near to the eggs (Wittmer and Ohba, 1994).

At night, the female emits weak continuous light from three small luminous organs on each body segment (Fig. 8.3). This unusual luminescent behavior is the only known example in the world and way be relevant to our understanding of the evolution of light signals.

THE COMMUNICATION SYSTEM OF *CYPHONOCERUS RUFICOLLIS*: CR SYSTEM

C. ruficollis flies during the day. Just after sunset, the male and female emit weak continuous light (Ohba, 1983*a*). Further, the male of this species has a small eye with reduced facets that receive light from a narrow acceptance angle. This species does not seem very suitable for long-distance communicating, but uses sex pheromones for sexual communication instead of flash signals. The weak continuous light is regarded as serving to locate mates locally when males and females approach and attempt to copulate at a dark

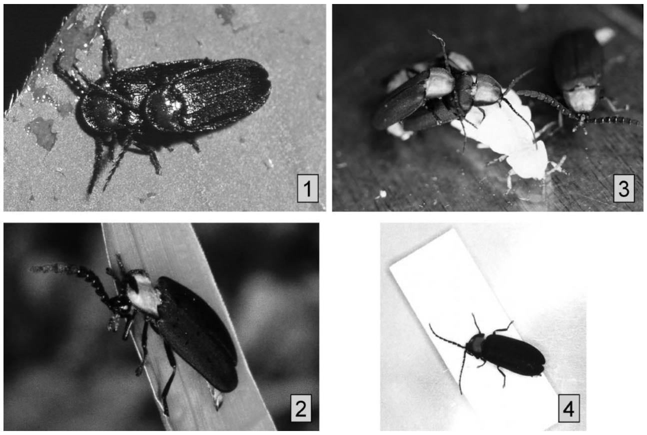

FIG. 9. Chemical communication of *Cyphonocerus ruficollis*, *Pyrocoelia abdominalis*, and *P. matsumurai*. 1. Copulation of *C. ruficollis*. 2. Orientation behavior of *P. abdominalis*. 3. A female attracts four males by her pheromone. 4. A small paper, which includes extracts of the female smell, attracts a male (Ohba, 1983*a*).

site such as the base of a grass stem just after sunset (Fig. 9.1). Communication in this species is summarized in Figure 11.

The following species possess a CR system based on field observations: *Cyphonocerus* fireflies and *Pyrocoelia fumoa*, *P. discicollis*, *P. matsumurai*, and *P. abdominalis* (Ohba, 1976, 1983*a*, 1997*a*, 1997*b*).

I have observed orientation behavior of male *P. abdominalis* in the field. The male stands on its legs, moves its antennae into a ''v'' position, and slowly swings his head (Fig. 9.2). In the laboratory, a female attracted four males during the daytime (Fig. 9.3) (Ohba, 1997*b*).

Orientation behavior of males is released by sex-attractants, as shown by n-hexane extracts of females.

ORIENTATION BEHAVIOR OF *PYROCOELIA MATSUMURAI*

Males perch on grass covered banks in woods. Almost all males approach females within 5 m downwind. When a male seeks a female, it stands on its legs and arranges its antennae in the form of a ''V.'' In this behavior, the male repeatedly swings its head very slowly and sometimes even flies a short distance. Thereafter the male repeats the same orientation behavior to seek a female, approaching slowly on a zigzag path (Ohba, 1997*a*).

In the orientation behavior, the male is always attracted to the head of the female, before copulation. It appears likely that the female emits a sex attractant, which acts as a releaser of male mating behavior (Ohba, 1997*a*).

Based on field and laboratory observations, the CR system is followed in this species. The male is also attracted by extracts of the female in n-hexane (Fig. 9.4) (Ohba, 1997*a*, *b*).

THE COMMUNICATION SYSTEM OF *LUCIDINA BIPLAGIATA*: LB SYSTEM

The adult of *L. biplagiata* is non-luminescent, but the larva emits continuous light from a pair of small light organs (Ohba, 1983*a*).

Male and female flight occurs during the day (Fig. 10). The antennae are well developed and the compound eyes are small, supporting the hypothesis that this species uses sex pheromones in sexual communication. Its flying area is generally narrow and limited. Thus seems that a flying male seeks a female, attracted, by pheromone.

The following genera are grouped under the LB system based on morphology and behavior: *Lucidina*, *Drilaster*, *Stenocladius*, and *Prystolycus* (Ohba, 1978).

Measurements of the size of the compound eyes and

FIG. 10. Copulation behavior of *Lucidina biplagiata* during the daytime (Ohba, 1983*a*).

TABLE 1. *Comparison of communication systems associated with behavior and morphology in the Japanese fireflies (Ohba, 1983a).*

COMMUNICATION SYSTEM		HP SYSTEM (SIGNAL SYSTEM II)	LL SYSTEM	LC SYSTEM (COMPLEX SYSTEM)	PR SYSTEM (SIGNAL SYSTEM I)	CR SYSTEM	LB SYSTEM
SIZE OF COMPOUND EYE e/p (OHBA, 1978)		0.80 - 0.70	0.80 - 0.70	0.70 - 0.65	0.45 - 0.27	0.30 - 0.27	0.22 - 0.20
SIZE OF ANTENNA log a/p (OHBA, 1978)		0.59 - 0.45	0.85 - 0.78	1.11 - 0.85	1.49 - 1.18	1.59 - 1 11	1.70 - 1.11
LUMINOUSTY	LARVA	++	++	+++	++++ - +	++ - +	++ - ±
	ADULT	++++	++++	+++++	++++ - ++	+	±
LUMINESCENT PATTERN		SINGLE SHORT PULSE	SINGLE PULSE	SINGLE LONG PULSE	CONTINUOUS LIGHT	CONTINUOUS WEAK LIGHT	NONLUMINESCENCE
ACTIVITY		NOCTURNAL	NOCTURNAL	NOCTURNAL	NOCTURNAL	AMPHIPETAL	DIURNAL
LUMINESCENT SIGNAL		CRITICAL TIMING FLASHES	NO CRITICAL TIMING FLASHES	NO CRITICAL TIMING FLASHES	+++++	+	-
CHEMICAL SIGNAL		-	-	±	+++++	+++++	+++++
SIZE OF LUMINOUS ORGAN		+++++	+++++	+++++	+++++ - ++	+	±
NOTE					FEMALE WINGLESS		

e/p: compound eye size scaled by pronotum size; a/p: antenna size scaled pronotum size; luminosity: − indicates non, + indicates weak, ++ indicates middle, ++++ indicates strong; luminescent signal: ++++ indicates strong continuous light, + indicates weak continuous light; chemical communication: − indicates non pheromone, ++++ indicates much pheromone; size of luminous organ: + indicates small, ++ indicates middle, ++++ indicates large.

antennae were made (Table 1) and compared to the typical communication system.

Aspects of the relationship between morphology and communication system of the fireflies are summarized below, based on data in Table 1.

The width of the antenna in diurnal and crepuscular-active fireflies is larger than that of nocturnally active fireflies. The length of sensilla in nocturnally active fireflies is greater than in diurnally active and crepuscular fireflies, but sensillar density on the antenna is higher in diurnal and crepuscular fireflies. The form of

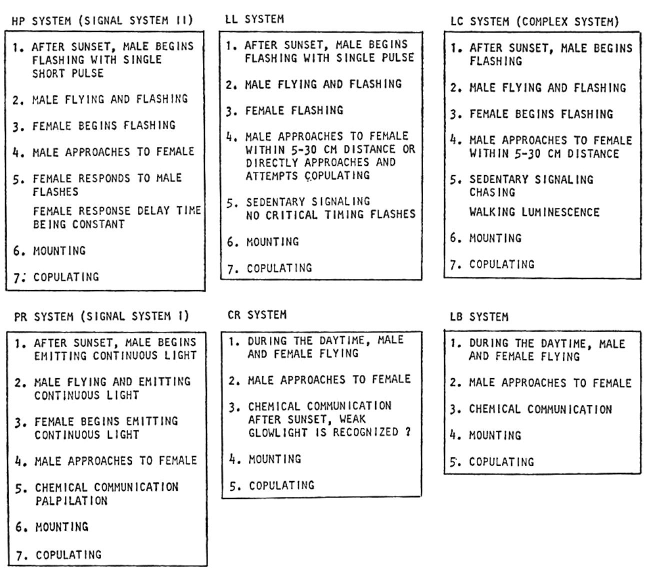

FIG. 11. Communication systems of Japanese fireflies (Ohba, 1983*a*).

the facets of the compound eye are irregular in diurnal fireflies, while in nocturnal fireflies, they are uniformly hexagonal.

Maxillary palps in nocturnal fireflies are somewhat larger than that of diurnal and crepuscular fireflies, and differ in form.

The inner face of the labial palps in nocturnal fireflies has three to five finger-like projections; while those of crepuscular and diurnal fireflies, are triangular or oval.

Short sensilla on the maxillary and labial palps, serve to recognize pheromone and touch when the male mounts the female (Matsuda and Ohba, 1991).

The luminescent signals of Japanese fireflies as analyzed by a new method based on computer analysis (Makino *et al.*, 1994) give results that are basically comparable to those which used a previous analysis system that employed analog data, but the time resolution and precision of the records were improved.

COMPARISON OF THE COMMUNICATION SYSTEM

The communication system of Japanese fireflies is classified into 6 types, namely HP System (Signal System II), LL System, LC System (Complex System), PR System (Signal System I), CR System, and LB System (Fig. 11), based on morphology and behavior.

For example, the compound eyes of the HP group are the largest in size compared with the LL, LC, PR, CR, and LB systems. These changes are accompanied by an activity change from diurnal to nocturnal activity (Table 1).

Sex pheromones are probably involved in the PR, CR, and LB Systems. The courtship pattern in *Pyro-*

coelia rufa resembles most the pattern in the European firefly *Lampyris noctiluca*.

Luminescent signals are found in the HP, LL, LC, PR, and CR systems. However the CR system depends mainly on a sex pheromone. The HP System has been described as Signal System II in American *Photinus* fireflies (Lloyd, 1966). This flash communication system involves a process of critical timing of the female flash responses to male flashes.

In the LL system, the mating behavior of males is induced by a flickering of light; in the LC system, males approach or leave a female while emitting various flash patterns. The female recognizes a male display and its various flash patterns. This communication system is similar to that found in the Papua New Guinea firefly *Luciola obsoleta* (Lloyd, 1971). LL system is specific Japanese firefly's communication. The LL system is not known in North American fireflies.

The PR system resembles Signal System I of Lloyd (1966). Most fireflies in this group emit a continuously glowing light which only reveals position. The flying male is attracted to the female's light. These fireflies use a pheromone in sexual communication. The CR and LB system fireflies use sex pheromones, but the former emits a very weak glowing light that is not suitable for communication between male and female.

The enlarged palps of males of several species, and the slight modification of the antennae in others, are associated with tactile displays. The members of this group are similar anatomically.

Geographical Distribution and Habitat Isolation

The geographical distribution of Japanese fireflies is summarized as follows: The *Cyphonocerus* group is uncommon in the most arid region of Japan. Exceptions are *C. inelegans*, known only from Mie prefecture, central Japan, and *C. yaeyamensis* from around Iriomote Island, Okinawa.

The *Drilaster* fireflies are almost all found in the southwestern islands of southern Japan with the exception of *D. axillaris*. The habitat of these species is limited.

Among *Luciola* fireflies, the most widespread species is *L. lateralis*, distributed throughout all Japan with the exception of Okinawa. *L. cruciata* lives near streams or rivers. *L. lateralis* lives in rice fields and are isolated in habitat. The other species are distributed in southern Japan.

L. kuroiwae is found in Okinawa and the Amami Islands. *L. yaeyamana* is found in Iriomote Island and Ishigaki Island. These species are isolated geographically.

In the genus *Hotaria*, *H. parvula* is widely distributed in Honshu, Shikoku, and Kyushu, while *H. tsushimana* is known only from Tsushima Islands in Nagasaki Prefecture.

In the genus *Curtos*, two species occupy different sides of Southwest Island. Nocturnal species of *P. rufa* are found only on Tsushima Island. *P. mayako* occurs only in Miyako Island. *P. atripennis* is found on Yaeyama Island, Okinawa.

Crepuscular species of *Pyrocoelia discicollis* is known from western Japan, but *P. fumosa* is found in northern Japan.

In *P. matsumurai*, *oshimana*, and *abdominalis*, each species is isolated by its geographical distribution.

In the genus *Lucidina*, the species have a local distribution, but *L. biplagiata* and *L. accensa* are sometimes found in the same habitat.

Seasonal Distribution

The seasonal distribution of adult fireflies is as follows: Most species are active during the summer.

In *Drilaster* species, emergence is in April on the southwest islands. *Pyrocoelia atripennis*, *matsumurai*, *abdominalis*, and *ohsimana* appear in May in the southwest island. *P. rufa* appears in September. *Rhagophthalmus ohbai* appears only in the winter season (Ohba, 1983*a*; Wittmer and Ohba, 1994).

Thus, Japanese fireflies do not isolate completely by seasonal distribution.

Sexual Isolation of Male Genitalia

In most Japanese fireflies, male genitalia are species-specific, but, in the genera *Pyrocoelia* and *Lucidina*, male genitalia are similar to one another (Ohba, 1983*a*, 1986). If different species are put in the same box, they readily copulate. Thus they cannot be isolated completely by the functional morphology of the male genitalia, but these species differ in habitat, seasonal prevalence, and geographical distribution.

How are Species Isolated?

Japanese fireflies are isolated by a combination of differences in their communication system, the functional morphology of their compound eyes, antennae, and male genitalia and /or their geographical and seasonal distribution.

Conclusion

1. The communication systems of Japanese fireflies are grouped into 6 types.
2. The communication systems are correlated with their morphology and behavior.
3. Japanese fireflies are isolated from each other in their communication system, functional morphology, genitalia, geographical and seasonal distribution.

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Yata Haneda, Emeritus Director of the Yokosuka City Museum, and my wife Shoko.

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