

Reflex bleeding of fireflies and prey-predator relationship

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ホタルの体液分泌と捕食者-被捕食者の相互関係

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Key words: firefly, Lampyridae, reflex bleeding, predator defensive system

キーワード: ホタル, ホタル科, 体液分泌, 捕食者、防御システム

Reflex bleeding phenomenon was clearly demonstrated in the Japanese fireflies. From experimental observations the response on predators of fireflies, predatorial behavior was observed in spiders and crabs. Further, evasive behavior was seen in raccoon-dog, bat, and gobies. Reflex bleeding, luminescence, death mimicry and their coloration are discussed in the context of prey-predator relationship. These behavior patterns will be very important in understanding the defensive systems in fireflies.

日本のホタルの体液分泌行動について明らかにした。ホタルの捕食者の野外観察を行うとともに、室内においてホタルの捕食者の反応を実験的に観察したところ、捕食行動はクモとカニに観察された。さらに、ホタルに対する忌避的な行動は、タヌキ、コウモリ、およびハゼ類ほかに見られた。ホタルの体液分泌行動と発光・擬死・体色パターンは、学習能力を有する捕食者に対しての防御機能を果たしていると考えられた。ホタルのこれらの行動様式は、防御システムの進化を理解する上に、重要な知見である。

Reflex bleeding of firefly has been reported in the north-American firefly, *Photinus pyralis* (BLUM and SANNASI, 1974). It was proposed that reflex bleeding is a defensive behavior against predators, however this idea is not enough demonstrated by field observations or experiments. This behavior and prey-predator relationship have been unknown in Japanese fireflies.

Therefore, the authors experimented and observed reflex bleeding and prey-

predator relationship in the Japanese fireflies in field and laboratory conditions (OHBA and HIDAKA, 1991). Furthermore, the authors experimented on prey-predator relationship on firefly larvae which did not so clearly show the reflex bleeding behavior. The authors observed and experimented with reflex bleeding in many species of Japanese fireflies. The behavior and relationship regarding reflex bleeding, luminescence, and their coloration are discussed in the

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paper. Knowledge of these behavior patterns will be important in considering defensive system in fireflies (LLOYD, 1973; MACLOSKIE, 1885; OHBA, 1986, 1988). In this study, some remarkable facts on the reflex bleeding and prey-predator relationship are clarified through research on Japanese fireflies.

Materials and method

Larvae and adults of Japanese fireflies observed in this study are listed in Table 1. Occurrence of reflex bleeding in fireflies was tested by pressing or stimulating their body and elytra with fingers or tweezers. Parallel to this, many specimens of fireflies deposited in Yokosuka City Museum were examined

for traces of blood and traces of discharge of blood.

On the other hand, some species of fireflies were experimentally confronted to some animals: mammals, frogs, fishes, spiders and crabs, in the field and laboratory. Predation behavior of reared raccoon-dogs was observed at the Experimental Forest, Kyoto University and at Yokosuka City Museum. Larvae of *Luciola cruciata* and *L. lateralis* emitting smell were subjected to a different experiment: First and last instar larvae of the fireflies were dropped into an aquarium and predation behavior of fresh water fish, *Rhinogobius brunneus* and larva of dragonfly, *Anotogaster sieboldii* SELYS was observed.

Table 1 Observation and collecting locality of fireflies.

Species of fireflies	Observation and collecting locality
Lampyridae	
Ototretinae	
<i>Drilaster</i>	
<i>D. axillaris</i> KIESENWETTER, 1879	Juniso, Kamakura City, Kanagawa Pref.
<i>Stenocladius</i>	
<i>S. azumai</i> NAKANE, 1981	Hyakuna, Tamagusuku Vill., Okinawa Pref.
Luciolinae	
<i>Luciola</i>	
<i>L. cruciata</i> MOTSCHULSKY, 1854	Nobi, Yokosuka City, Kanagawa Pref.
<i>L. owadai</i> M. SATO et M. KIMURA, 1994	Kumejima Is., Okinawa Pref.
<i>L. lateralis</i> MOTSCHULSKY, 1874	Nobi, Yokosuka City, Kanagawa Pref.
<i>Hotaria</i>	
<i>H. parvula</i> KISENWEETTER, 1874	Naoya City, Aichi Pref.
Lampyrinae	
<i>Pyrocoelia</i>	
<i>P. rufa</i> E. OLIVIER, 1886	Izuhara, Tsushima, Nagasaki Pref.
<i>P. miyako</i> NAKANE, 1981	Kurima Is., Miyako Isls., Okinawa Pref.
<i>P. atripennis</i> LEWIS, 1896	Kabira, Ishigaki Is., Okinawa Pref.
<i>P. discicollis</i> KIESENEWETTER, 1874	Omogokei, Ehime Pref.
<i>P. fumosa</i> GORHAM, 1883	Juniso, Kamakura City, Kanagawa Pref.
<i>P. matsumurai</i> NAKANE, 1961	Yona, Kunigamigun, Okinawa Pref.
<i>P. abdominalis</i> NAKANE, 1985	Kabira, Ishigakijima, Okinawa Pref.
Lucidina	
<i>L. biplagiata</i> MOTSCHULSKY, 1866	Juniso, Kamakura City, Kanagawa Pref.
<i>L. accensa</i> GORHAM, 1883	Omogokei, Ehime Pref.

Results

Reflex bleeding

Traces of reflex bleeding of the fireflies were found on the margins of the elytra, pronotum and antennal sockets (Fig. 1). In one of our observations, 8 traces of discharged blood were found on the elytra and one on the frontal margin of pronotum of male *Pyrocoelia atripennis* (Fig. 1-1, 2). In male of *P. miyako*, and in male of *P. rufa*, one trace each was found on the elytra (Fig. 1-3, Fig. 1-4). In male *Luciola cruciata*, 3 traces on the elytra (Fig. 1-5), in adult *Lucidina biplagiata*, 2 on the elytra (Fig. 1-6) and in adult of *L. accensa*, one on the elytra (Fig. 1-7, 8). Blood is discharged at the site closest to the source of tactile stimulation. Traces of reflex bleeding were thus observed at similar sites among different species of fireflies.

On the other hand, almost all the larvae of fireflies did not discharge blood, but in *L. cruciata* and *L. lateralis*, when stimulus was applied to the larvae, they projected their white glands from each segment of their abdomen and emitted a defense substance from the extruded gland (Fig. 2).

Reflex bleeding in adult fireflies was observed predominantly in diurnal species, and in some nocturnal species. We confirmed the traces of reflex bleeding in the center of elytral suture and margin of epipleuron from traces dried blood (Fig. 3).

Based on our many observations, the traces distribution of reflex bleeding in male adults of *P. atripennis* are shown in Fig. 4. Two traces were found on the antennal sockets, 15 on the margin of the elytra, and one on the caudal segment (Fig. 4-6).

Defense secretion of female adult of *P. atripennis* which lacks wings was

observed. A reflex bleeding site on the pronotum of a female adult of *P. atripennis* was determined, but no traces of bleeding observed on the abdomen.

In *P. miyako*, 2 traces were found on the antennal sockets, and 12 on the margin of the elytra (Fig. 4-5). In *P. rufa*, 13 traces were found on the elytra (Fig. 4-7). We also observed by the same methods the behavior of *P. fumosa*, *P. discicollis*, *Lucidina biplagiata* and *L. accensa*. In *P. fumosa*, 15 traces were found (Fig. 4-2), in *P. discicollis*, 5 on the elytral margins (Fig. 4-3) and in *P. matsumurai*, 2 on the pronotum and 12 on the elytral margin (Fig. 4-4). In *Lucidina biplagiata* and *L. accensa*, 2 traces were found on the antennal sockets of pronotum, and 9 and 12 on the elytra (Fig. 4-8, 9). Among nocturnal species of the fireflies, reflex bleeding was observed in *L. cruciata*, 8 traces were found on the margin of the elytra and one on the caudal segment (Fig. 4-1). Adult of *L. cruciata* discharged a pale yellowish white secretion from sites surrounding the elytra when the firefly was pressed. We confirmed some blood-discharging sites (Fig. 4), but there may be still other site. The discharged blood emitted a smell and soon formed a hard crust which eventually flaked off the bodies.

When tactile stimulation was applied to the body of the firefly, most of the blood was discharged from the site to the region stimulated.

Thus defensive behavior was clearly observed in diurnal and crepuscular species which emit very weak or continuous light.

Reflex bleeding was not so clearly observed in the larvae.

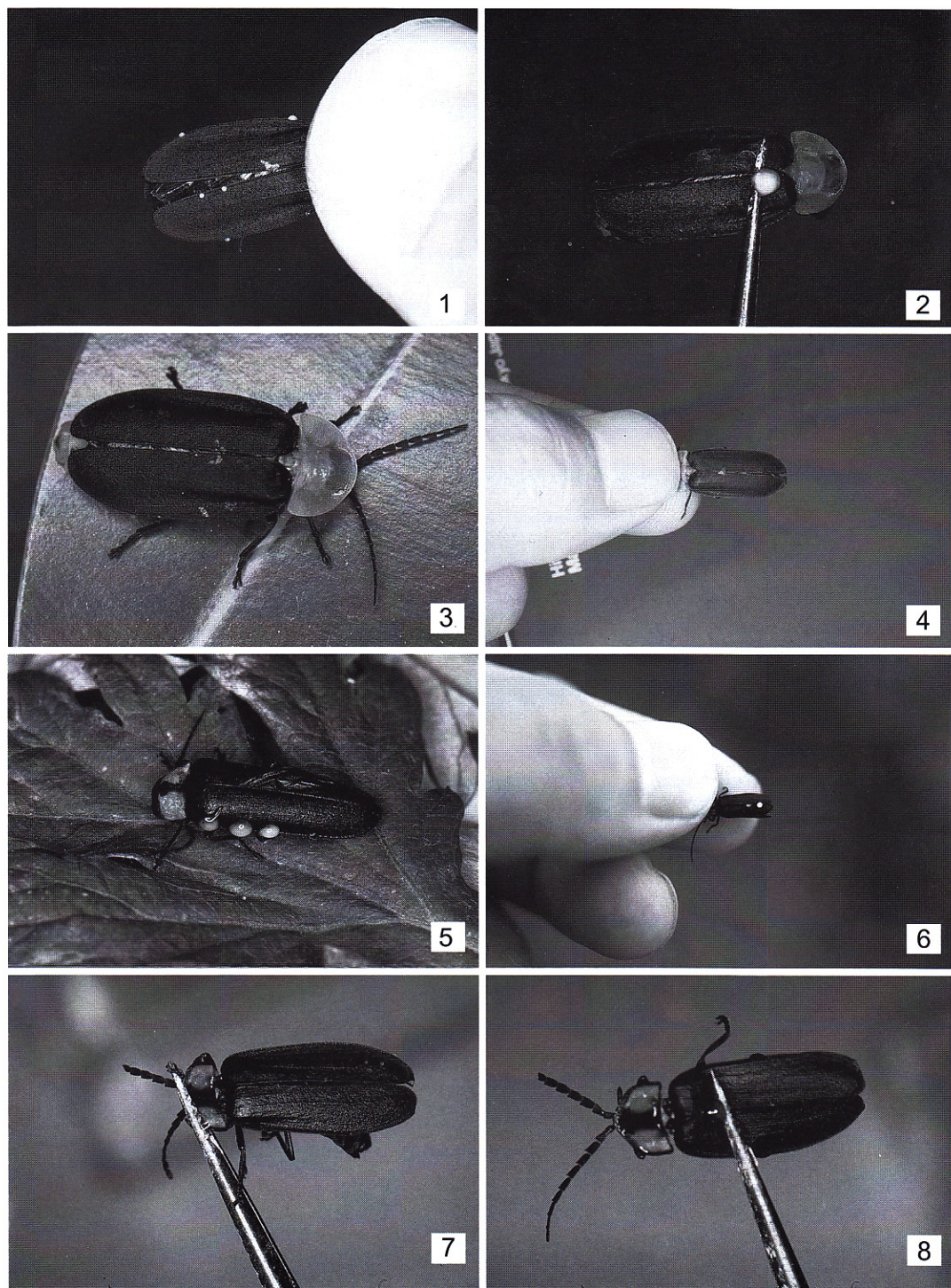


Fig. 1 Discharges from the margin of elytra and pronotum of fireflies.
 1-2. Male of adult *Pyrocoelia atripennis*, 3. Male of adult *P. miyako*, 4.
 Male of adult *P. rufa*, 5. Male of adult *Luciola cruciata*, 6. Adult of
Lucidina biplagiata, 7-8. Adult of *L. accensa*.



Fig. 2 Larva of *L. cruciata* projected their white glands from each segment of their abdomen and emitted a bad smell from the extruded gland.

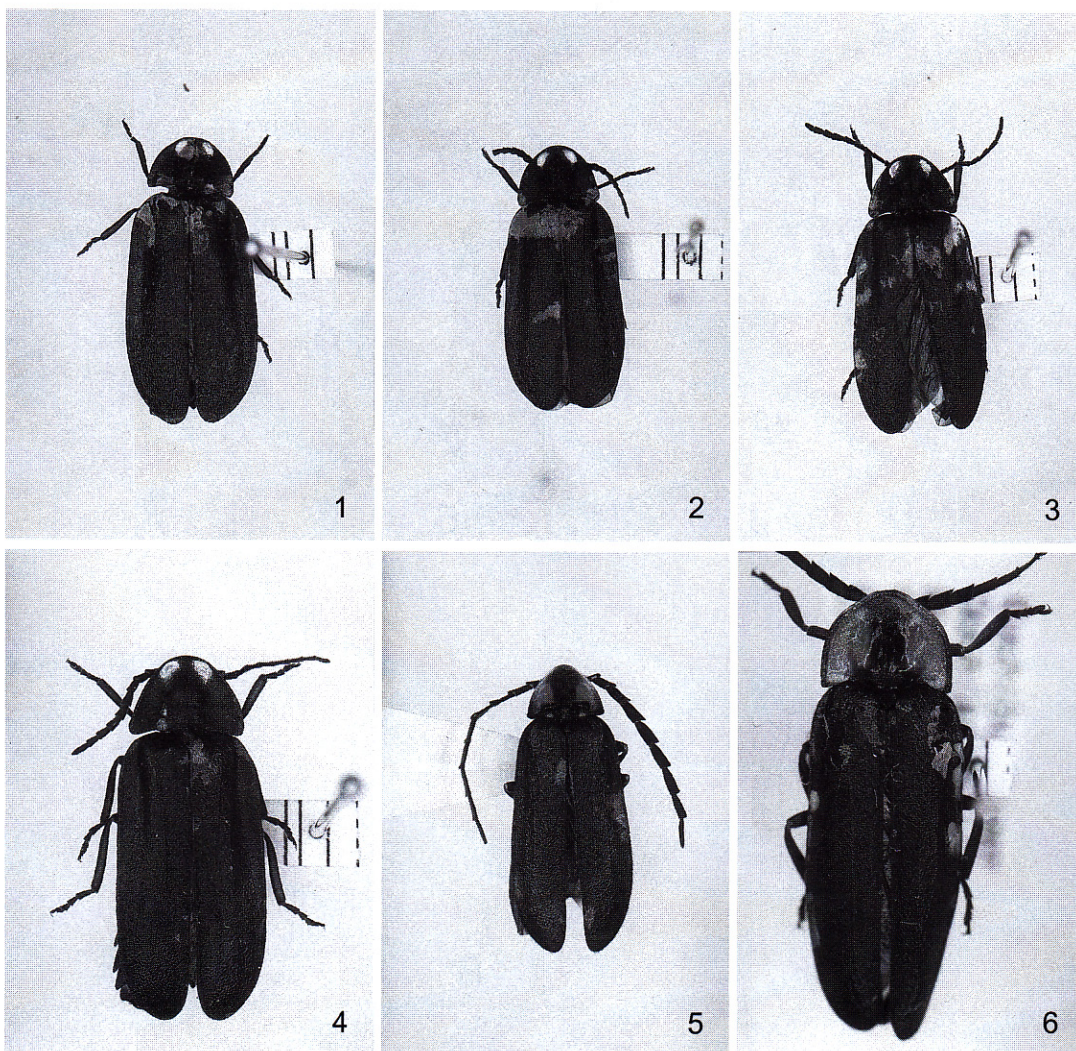


Fig. 3 Dry blood traces on the elytra and pronotum of the dry specimens of the fireflies.
1-4. Adults of *Pyrocoelia fumosa*, 5. Adult of *Lucidina biplagiata*, 6. Adult of *L. accensa*.

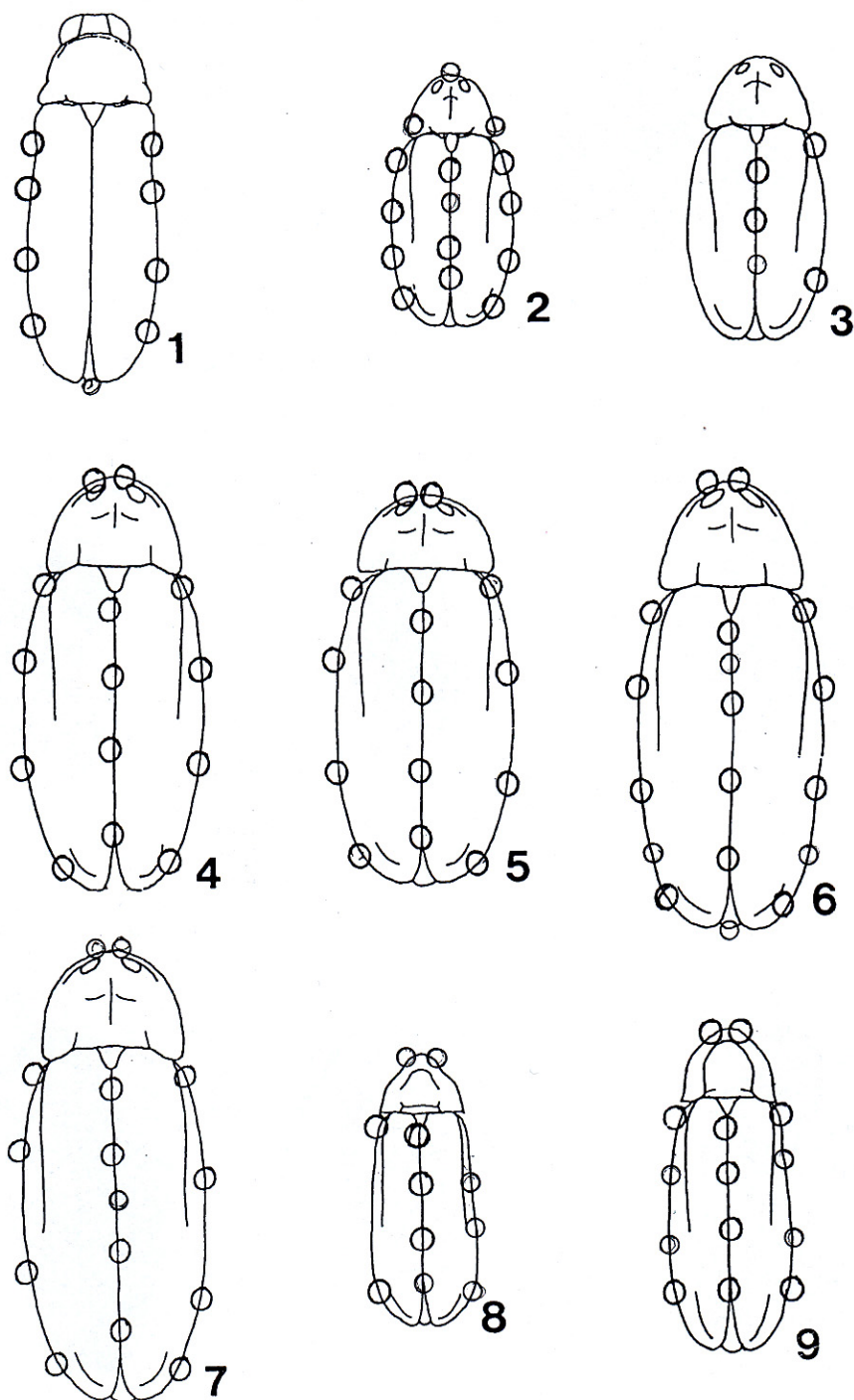


Fig. 4 Distribution of points of reflex bleeding in male fireflies.
 1. *Luciola cruciata*, 2. *Pyrocoelia fumosa*, 3. *P. discicollis*. 4. *P. matsumurai*,
 5. *P. miyako*, 6. *P. atripennis*, 7. *P. rufa*, 8. *Lucidina biplagiata*, 9. *L.*
accensa.

Prey-predator relationship

In laboratory observations, the freshwater goby, *Rhinogobius brunneus* and the larva of the dragonfly, *Anotogaster sieboldii* bit immature larvae of *L. lateralis* and *L. cruciata*, but they immediately vomited the larvae, and they never attempted to bite them again. The larvae of *L. cruciata* and *L. lateralis* expanded and protruded their glands from their each abdominal segment. Then they emitted a bad smell from the glands.

Data on experimental prey-predator relationships are presented in Table 2.

We observed that ants attacked and pulled weakened adult female of *L.*

cruciata which did not discharge blood.

A crab, *Patamon (Geothelphusa) dehaani* caught an adult of female *L. cruciata* which was emitting light. Then the crab immediately brought it into the nest (Fig. 5-1). The next day, only elytra of the firefly was left in the nest of the crab.

Adult males of *Pyrocoelia rufa* were caught by spiders in webs, and *P. atripennis*, *P. miyako*, *Hotaria parvula*, *Luciola owadai* and *L. lateralis* were attracted to the light of the fireflies that were caught by spider (Fig. 5-2, 3, 4). Wandering spiders also ate adults of *P. atripennis*, *P. miyako*, *H. parvula*, *C. okinawana*, *Luciola owadai* and *L.*

Table 2 Experimental prey-predator relationship.

Predator	Prey (firefly)	Predation	Notes
raccoon dog	adult of <i>Pyrocoelia atripennis</i>	evasion	force feed
	larva of <i>P. atripennis</i>	evasion	force feed
	larva of <i>P. okinawana</i>	evasion	force feed
bat	larva of <i>P. atripennis</i>	vomit	force feed
	larva of <i>P. okinawana</i>	refusal	force feed
toad	larva of <i>P. atripennis</i>	swallow	force feed
	larva of <i>P. okinawana</i>	swallow	force feed
larva of dragonfly	larva of <i>Luciola cruciata</i>	vomit	force feed
	larva of <i>L. lateralis</i>	vomit	force feed
goby	larva of <i>L. lateralis</i>	vomit	force feed
	larva of <i>L. cruciata</i>	vomit	force feed
small crab	adult of <i>L. cruciata</i>	capture and eat	prey emitting light
spider	adult of <i>L. cruciata</i> (♂, ♀)	capture and eat	prey emitting light
spider	adult of <i>L. cruciata</i> (♂, ♀)	capture and eat	prey emitting light
centipede	adult of <i>Lucidina biplagiata</i> (♂)	capture and eat	observed in daytime
mantis	adult of <i>Pyrocoelia rufa</i> (♀)	capture and eat	prey emitting light
ant	adult of <i>L. cruciata</i> (♀)	attack	prey emitting light
ant	adult of <i>P. miyako</i> (♂)	attack	reflex bleeding
ant	larva of <i>Stenocladus azumai</i>	attack	reflex bleeding
leech	adult of <i>L. cruciata</i>	capture and eat	(KURIBAYASHI, 1977)
spider	adult of <i>Hotaria parvula</i> (♂)	capture and eat	prey emitting light
spider	adult of <i>Pyrocoelia rufa</i> (♂)	capture and eat	prey emitting light
spider	adult of <i>P. miyako</i> (♂)	capture and eat	prey emitting light
spider	adult of <i>Curtos costipennis</i>	capture and eat	prey emitting light
spider	adult of <i>C. okinawana</i> (♂, ♀)	capture and eat	prey emitting light
spider	adult of <i>Luciola kuroiwae</i> (♂)	capture and eat	prey emitting light
spider	adult of <i>Luciola yayeyamana</i> (♂)	capture and eat	prey emitting light
spider	adult of <i>Luciola owadai</i>	capture and eat	prey emitting light

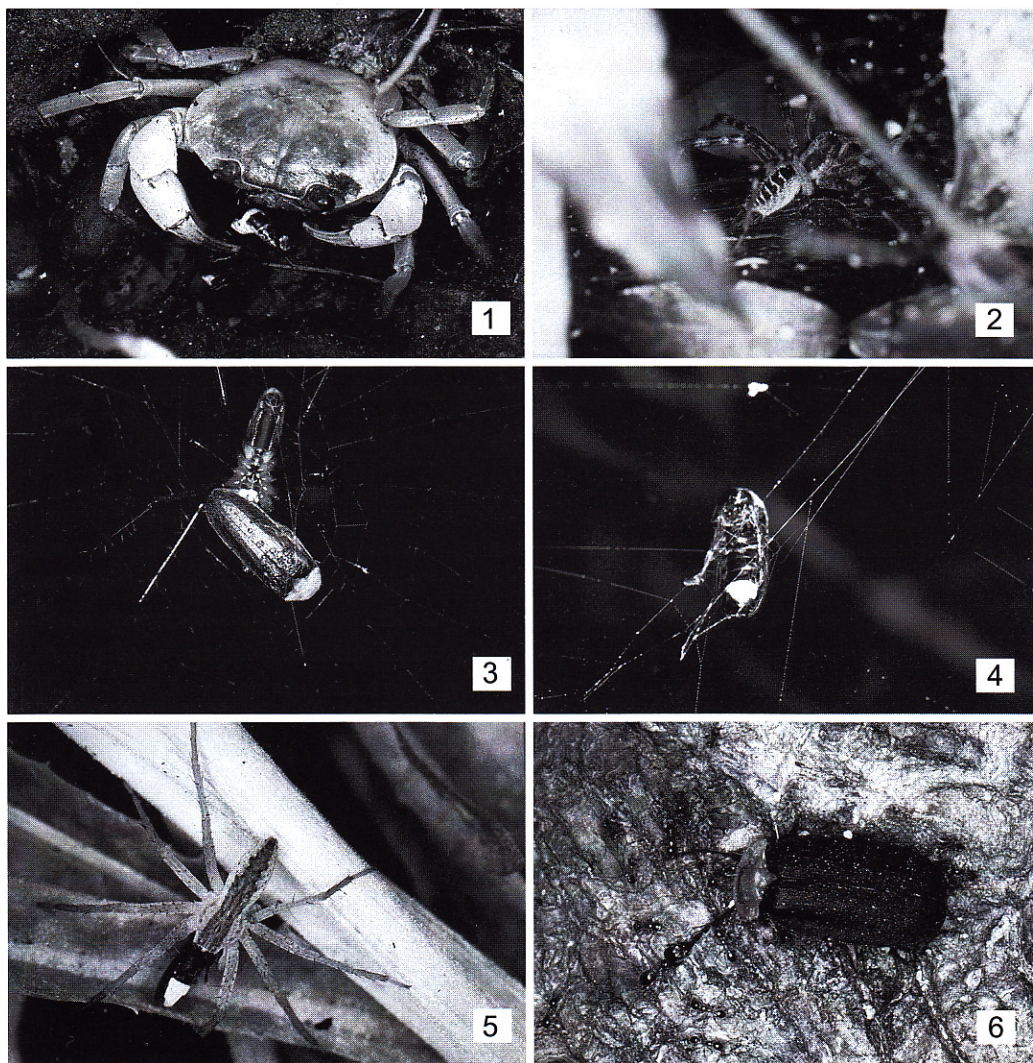


Fig. 5 Predators of the fireflies in the field and laboratory observations.

1. Crab captured and ate an adult of *Luciola cruciata*, 2. A spider captured an adult of *L. cruciata*, 3. Adult of *L. owadai*, 4. Adult of *L. lateralis*, 5. Adult of *Hotaria parvula*, 6. Adult of *Pyrocoelia miyako* discharged blood from the margin of the elytra when many ants gathered to the firefly.

cruciata (Fig. 5-5). Raccoon-dogs did not capture the larvae of *Pyrocoelia fumosa* and *P. abdominalis* which were presented in front of them.

Evasive action was observed in the bat, *Myotis macrodactylus*, when larvae of the fireflies, *P. atripennis* and *P. abdominalis*, were given compulsively. When the bat ate the prey, they

immediately vomited it. Thereafter the bat avoided the prey and never tried to eat it.

Frogs, *Rana ornativentris* ate larvae of *Pyrocoelia atripennis* and *P. abdominalis* after being presented for a day, but they showed no interest to them (Fig. 6). However, the toad, *Bufo japonicus japonicus*, immediately swallowed larvae



Fig. 6 Frogs, *Rana ornativentris* did not soon eat a larva of *Pyrocoelia abdominalis*.



Fig. 7 Larva of *Stenocladus azumai* discharged blood from the body when many ants gathered to the larva.



Fig. 8 Diurnally active species of firefly, *Lucidina biplagiata* bitten by a centipede after the firefly exuded liquid from the elytra.

of *P. atripennis* and *P. okinawana* when the larvae were moved in front of the toad.

One of the authors, Ohba observed many ants gathered around very weakened adult male of *P. miyako* (Fig. 5-6) which could not move.

However, the ants avoided sites of discharged blood. A larva of *Stenocladus azumai* which discharged blood around own body (Fig. 7). Ants in the field avoided the larva and never attacked.

Table 3 Coloration of elytra and pronotum and activity of fireflies.

Species of fireflies	Color of elytra and pronotum	Activity	Flash pattern
<i>Drilaster axillaris</i>	elytra frontal margin small red spot	durnal	weakly continuous
<i>Luciola cruciata</i>	pronotum pink	nocturnal	brightly slow flashing
<i>L. lateralis</i>	pronotum pink	nocturnal	flashing
<i>Hotaria parvula</i>	pronotum pink	nocturnal	brightly fast flashing
<i>Pyrocoelia rufa</i>	pronotum yellow	nocturnal	brightly continuous
<i>P. miyako</i>	pronotum yellow	nocturnal	brightly continuous
<i>P. atripennis</i>	pronotum and abdomen reddish yellow	nocturnal	brightly continuous
<i>P. discicollis</i>	pronotum red	crepuscular	weakly continuous
<i>P. fumosa</i>	body black	durnal	weakly continuous
<i>P. matsumurai</i>	pronotum red	crepuscular	weakly continuous
<i>P. abdominalis</i>	pronotum and abdomen pink	crepuscular	weakly continuous
<i>Lucidina biplagiata</i>	pronotum pink	durnal	none luminescent
<i>L. accensa</i>	pronotum pink	durnal	none luminescent
<i>Pristolytus sagulatus</i>	elytra vivid red	durnal	none luminescent

In the daytime, Ohba observed that small centipede attacked an adult of *L. biplagiata*, then the firefly discharged blood (Fig. 8).

Activity and coloration of elytra and pronotum of fireflies are shown in Table 3. Almost all of fireflies have vivid color and emit light at night.

Discussion

Reflex bleeding

BULUM and SANNASI (1974) reported on the reflex bleeding system utilized by *Photinus pyralis*. According to their report, lampyrids appear to autohaemorrhage at sites on the pronotal and elytral margins, as well as the area around the antennal sockets. Furthermore, they mentioned that, because of the presence of reflex bleeding are as around the antennal sockets, it is guaranteed that a small predator will be greeted with a lampyrid bloodbath if it initially contacts the head of the firefly. They considered that the fact that rapidly coagulating blood of *P. pyralis* deters fire ants demonstrates that this defensive system is highly adaptive against small predator insects.

In Japanese fireflies, traces of discharged blood were found on the margin of elytra and pronotum. This is very similar to American firefly species.

All the sites of reflex bleeding of fireflies could not be determined in our study, but our observation indicates that the sites of reflex bleeding are similar in many species of fireflies.

Reflex bleeding sites surround body of fireflies, therefore a small predator may be difficult to attack a firefly. When a firefly becomes weak and can not move, the firefly can not discharge the blood. In such cases, the firefly will be eaten by small predators including ants. On

the other hand, the amount of blood secreted is associated with the stimulus. When the stimulus is applied to fireflies, more blood is secreted from the position closet to the stimulated site. This defensive mechanism is suitable against predators.

Prey-predator relationship and defensive system

In the Japanese fireflies, same defensive system as the American fireflies was observed. We saw many ants gathered around an adult male of *P. miyako*, *L. cruciata* and the larva of *Stenocladus azumai* which discharged blood from the body. Then the ants avoided the blood. This defensive system is adaptive against small predator including ants.

WILLIAMS (1917) reported that many fireflies exude blood from the elytra and pronotum, as well as from the coxal joints. Further, meloids and coccinellids exhibit reflex bleeding from the femoro-tibial joints (HAPP and EISNER, 1933; WHITEMORE and PRUESS, 1982). Based on our field and experimental observations, we confirmed that fireflies exhibit reflex bleeding from the antennal sockets, margin of elytra, pronotum and caudal segment. Our field and experimental observations also show that reflex bleeding of fireflies is closely associated with luminescence when captured by predators. It appears that reflex bleeding is an adaptive behavior in protecting them against predators, such as insects, birds and mammals.

Raccoon-dogs and bats have learning ability, and these animals learn that fireflies are bad-taste prey and reflex bleeding is associated with coloration of body and luminescence (Table 3). Therefore, they never capture again the prey with such coloration. However, the

reflex bleeding and luminescence are not effective defensive behavior against spiders, centipedes and crabs, because these animals are believed to have poor learning ability. Lampyrids appear to autohaemorrhage at sites on the pronotal and elytral margins, as well as the area around the antennal sockets. The reflex bleeding appears to occur at many sites on the body of a firefly. Therefore, if a predator bites any site of the body, blood is exuded from the closet position to the site. This is a suitable defensive behavior against predators.

Relationship of coloration and reflex bleeding in diurnal fireflies

Among diurnal species of fireflies, *Lucidina biplagiata* and *Pyrocoelia fumosa*, reflex bleeding can be recognized conspicuously. There are many predators in the daytime. Reflex bleeding and vivid coloration may have more significance in protecting fireflies against predators which have learning ability. This is so because when a predator captures a prey with vivid color, they learn the taste, smell and color of the prey. They will never capture thereafter the prey with vivid colors.

Generally, diurnally active species of fireflies emit very weak light or are not luminescent. Vivid coloration in diurnally active species of fireflies is associated with reflex bleeding and exhibit defensive effects as warning signals against diurnally active predators.

Example: adults of *Pristolycus sagulatus* and *Drilaster ohbayashii* have vivid red color on the dorsal side, and the adult of *Pyrocoelia abdominalis* also has a vivid pink pronotum.

Insect coloration is an important factor in determining the acceptability of insects to birds (JONES, 1932). Vivid

coloration of adults serves effectively as part of the firefly's defensive system.

In the larvae of *P. atripennis* and the other species, reflex bleeding has not been documented, but, death mimicry is clearly observed.

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