SEX PHEROMONE AND PATTERN OF MATING COMMUNICATION OF FIREFLIES IN SUBFAMILY LAMPYRINAE (COLEOPTERA: LAMPYRIDAE)

Wandee Wattanachaiyingcharoen[1*] Winyoo Phanmuangma[2]
Surat Boonphong[3] Nungruthai Suphrom[3] and Surisak Prasanpan[4]

[1]Department of Biology and Center of Excellence for Biodiversity, Faculty of Science, Naresuan University
[2]Naresuan University Secondary Demonstration School, Naresuan University
[3]Department of Chemistry, Faculty of Science, Naresuan University
[4]Faculty of Medical Sciences, University of Phayao
[*]corresponding author e-mail: wandeew@nu.ac.th

(Received: 17 April 2020; Revised: 7 May 2020; Accepted: 8 May 2020)

Abstract

Fireflies in the subfamily Lampyrinae are recognized as glow-worms because they emit continuous green light for sexual communication. Many reports revealed that those glow-worms combined continuous glow with chemical secretion in mating encounters. Four species of fireflies including *Diaphanes* sp.1, *Diaphanes* sp.2, *Pyrocoelia praetexta* and *Lamprigera tenebrosa,* were investigate their specific pattern of mating communication. The chemical secretions from female fireflies were collected during their mating time to determine the chemical components using GC-MS analysis. Also, we observed the morphological characters related to mating behavior. The sex pheromones of *Diaphanes* sp.1 and *Diaphanes* sp.2 consisted of six chemical components (hydrocarbons) with four similar chemicals; tetracosane, pentacosane, hexacosane and heptacosane. However, the sex pheromone from *P. praetexta* comprised of only one unidentified chemical whereas *L. tenebrosa* showed no detection of any chemicals. These results indicated that these firefly species used a specific chemical clue for sexual communication within generic and species levels. The observations of morphological characteristics showed that males in all species, except *L. tenebrosa*, possess complex antennae, which assist in the chemical communication. The results indicated that fireflies in the subfamily Lampyrinae had a variation in mating communication. The first group communicates by emitting the continuous light combine with sex pheromone (*Diahanes* sp.1, *Diaphanes* sp.2

and *Pyrocoelia praetexta*) and the second group (*L. tenebrosa*) solely employs brighter glow in sexual communication.

Keywords: Firefly, Lampyrinae, Mating communication, Insect sex pheromone

INTRODUCTION

Fireflies in the family Lampyridae are well recognized as they possess a unique characteristic called a light organ which is used to produce bioluminescence (McDermott, 1966). Adult nocturnal fireflies are familiar with their capability of emitting intraspecific bioluminescence to attract the opposite sex (Lloyd, 1971). Differing flash patterns play a major role in natural reproductive isolating mechanisms, which reduces cross-species reproduction; particularly in some sympatric species (Lewis & Cratsley, 2008). However, not only flashing bioluminescence is used for reproductive communication, but also continuous light emission (Glow) is reported in several species. Besides, the use of continuous light combined with a sex pheromone for intra-species communication had been reported in some species of fireflies which cannot produce flashlight (Lloyd, 1997; Stanger-Hall, 2007). Those which produce continuous light were taxonomically classified into subfamily Lampyrinae while flashing light was performed by members of subfamily Luciolinae.

In northern Thailand, some nocturnal fireflies in the subfamily Lampyrinae, i.e. genera *Diaphanes, Pyrocoelia* and *Lamprigera* were reported as sympatric species. Their morphological appearances are distinguished (Jeng, 2008; Nak-aeim, 2015). From our previous observations, both male and female fireflies in these genera emit continuous light in courtship communications (Phanmuangma & Wattanachaiyingcharoen, 2017). It is difficult for the receivers to distinguish the signals due to the continuous light of glow-worms. The question arises that how these glow-worms distinguish their mates, especially in sympatric species. Stanger-Hall (2007) proposed that those fireflies who do not perform blinking flash in sexual communication might combine continuous luminescence with other clues such as chemical secretions or pheromones. The use of chemical signals especially in sexual communication has been reported in several firefly species, for example, *Phosphaenus hemipterus* (De Cock & Matthysen, 2005) and *Pyrocoelia oshimana* (Shibue et al., 2000). On the other hand, the morphological characteristics of male fireflies that use pheromones for communication typically possess large or well-developed antennae and small compound eyes (De Cock & Matthysen, 2005; Lloyd, 1997; Ohba, 2004). An important role of insect antennae is a chemoreceptor; they are used for receiving of chemical odors. Insect pheromones are released in a form of chemical molecules and are detected by sensillae in the antennae of receivers. These chemical molecules are interpreted and activated the compatible neurons, leading to an appropriate response (Van der, Goes van Naters & Carlson, 2006). The complex, large antennae can function in the sensing of odors released from senders, which are obvious in many firefly species (Branham & Wenzel, 2000; 2003). For example, *Phosphaenus hemipterus* and *Pyrocoelia oshimana* possess large compound eyes and long antennae. However, contrary to those species, male fireflies in the genus *Lamprigera* possess large compound eyes but short antennae. It is, therefore, unresolved that fireflies in this genus use pheromone or other means for sexual communication. Additionally, the difference between fireflies in the genus *Lamprigera* and other glow-worms in the same subfamily is that they emit a brighter glow than other genera. This raises a question about which signals of those sympatric fireflies in these three genera use to recognize other members of their species and prevent cross-species mating.

The differences in chemical compositions of insect pheromones were reported among each insect species. For example, the chemical composition of pheromones from a moth species, *Chilecomadia valdiviana* were determined and four chemical compositions were identified; i.e. (7Z,10Z)-7,10-hexadecadienal; (Z)-7-hexadecenal; (Z)-9-hexadecenal and (9Z,12Z)-9,12-octadecadienal (Herrera et al., 2016). Meanwhile, (Z)-11-tetradecenyl acetate and (E)-9-dodecenyl acetate were found in the pheromone from another species of moth, *Proeulia triquetra* (Bergmann et al., 2016). These results suggested that sex pheromones produced by different insect species contain dissimilar chemical components, allowing to distinguished species-specific communication. In addition, Shibue et al. (2000) reviewed the analysis of female sex pheromones of firefly *Pyrocoelia oshimana* using GC-MS and found that it is composed of two chemicals, (Z)-9-tricosene and tricosane. The hydrocarbon compound, (Z)-9-tricosene, is quite common sex pheromones in many insect taxa. This chemical was reported as a component from the female sex pheromone of the house fly (*Musca domestica*) (Carlson et al., 1971), and from the male sex pheromone of the giant danaine butterfly, *Idea leuconoe* (Nishida et al., 1996).

In this research, we pursued the clues that those three genera of sympatric fireflies in the subfamily Lampyrinae employ in sexual communication and determined the chemical compositions of female sex pheromones using GC-MS analysis. In addition, bioluminescent schemes and related morphological characters of those species were examined.

MATERIALS AND METHODS

1. Bioluminescence observations and specimen collections

We surveyed fireflies in the subfamily Lampyrinae in northern Thailand and found four species of fireflies. The luminescent patterns of both adult male and female fireflies were observed and recorded in their habitats. We collected 16 adult female fireflies; i.e. three females of the *Diaphanes* sp.1, four females of the *Diaphanes* sp.2, four females of the *P. praetexta* and five females of the *L. tenebrosa.* All specimens were kept in plastic boxes and transferred to an insect rearing room. The conditions of the insect rearing room were maintained at 25 °C with a 12 : 12 (L : D) period.

2. Pheromone extraction

The techniques from Shibue et al. (2000) were modified and used for the detection of chemical components. In preparation, glass vials were washed with hexane and dried in an electric oven. During natural mating time, mostly from 18.30 to 20.30, an individual adult female firefly of each species was kept in the prepared vial for two hours. After that, the fireflies were removed from the vials. We added 1 ml of CH_2Cl_2 to each vial and shook the vial several times to dissolve the volatile chemicals released by the female fireflies. Each female firefly was treated in the same procedure for four times within four inclusive days.

3. Pheromone detection

The detection of chemical compounds in sex pheromones of observed fireflies was performed by GC-MS analysis, using a Hewlett Packard (Agilent Technologies, Palo Alto, CA, USA) gas chromatograph model 6890, equipped with a mass selective detector (MS). A fused silica capillary Hewlett Packard HP-5 (5% phenyl methyl siloxane) column (30 m x 0.25 mm i.d., 0.25 µm film thickness) was used for the GC separation. High purity helium was used as the carrier gas, with a constant flow rate of 1.0 mL/min. The injector was set at 250 °C and performed in split mode with a split ratio of 10 : 1 v/v. The initial oven temperature was held at 50 °C for 1 minute, then programmed at 20 °C/min to 280 °C and finally held at 280 °C for 10 minutes. The temperature of the transfer line heater was set to 280 °C. The mass scanning range was set to 50–550 am in full scan. The identification of volatile components was performed by matching their recorded mass spectra with that of the standard libraries; Wiley 7 n. Statistically, the matches fell within a 95% confidence level will be accepted.

RESULTS AND DISCUSSION

1. Bioluminescence observations and related morphological characters

Our observations on firefly bioluminescence in the field revealed that during the courtship period, both males and females of all four firefly species emitted continuous glowing light instead of flashing light, which was similar to the previous report by Phanmuangma & Wattanachaiyingcharoen (2017). *L. tenebrosa* performed a very bright green glow compared to other observed species. The comparison of the illumination pattern and light organs of those four firefly species is shown in Figure 1 and Table 1. The females of *Pyrocoelia praetexta* possesd less-developed wings (brachypterous females) while the females of *Diaphanes* sp.1, sp.2, and *L. tenebrosa* had no wings. The antennae of males in *Diaphanes* spp. and *P. praetexta* were relatively longer compared to the obviously shorter antennae in males of *L. tenebrosa*. The insect antennae are in charge as a chemoreceptor, therefore, the complex of antennae maybe play an important role in chemical receivers (Branham & Wenzel, 2000; 2003). Hence, longer antennae in the males of *Diaphanes* spp. and *P. praetexta* indicated that they use their complex antennae in specific communication via chemical odors.

Figure 1 Male and female fireflies, a) male of *Pyrocoelia praetexta*, b) female of *P. praetexta* with the less-developed wings, c) male of *Lamprigera tenebrosa*, and d) female of *L. tenebrosa* without developed wings. (Note the luminescence of a), c), d))

Table 1 Illumination pattern of four firefly species; *Diaphanes* sp.1, *Diaphanes* sp.2, *P. Praetexta* and *L. tenebrosa.*

Firefly species	Illumination pattern
Diaphanes sp.1	glow
Diaphanes sp.2	glow
P. praetexta	glow
L. tenebrosa	bright glow

2. Pheromone detection

We collected and extracted sex pheromones from adult females of four firefly species. The GC-MS process was repeated four times for each individual firefly. The complete ion chromatogram of the volatile components from the sex pheromones of each firefly species is shown in Figure 2. The chemical composition of sex pheromone of these fireflies composed of hydrocarbons. The analysis of sex pheromone of the *Diaphanes* sp.1 exhibited six chemical compounds that occur at the retention times of 10.57, 11.00, 11.42, 11.84, 12.30 and 12.82 min. respectively (Figure 2, a)). The comparison of provided chemicals with the standard libraries referred to these chemicals as docosane ($C_{22}H_{46}$), tricosane ($C_{23}H_{48}$), tetracosane ($C_{24}H_{50}$), pentacosane ($C_{25}H_{52}$), hexacosane ($C_{26}H_{54}$) and heptacosane ($C_{27}H_{56}$) (Table 2). Similarly, we detected six chemical components from the sex pheromones of *Diaphanes* sp.2 at the retention time of 12.41, 12.83, 13.29, 13.82, 14.43 and 15.16 min. respectively (Figure 2, b)). They were classified as tetracosane ($C_{24}H_{50}$), pentacosane ($C_{25}H_{52}$), hexacosane ($C_{26}H_{54}$), heptacosane ($C_{27}H_{56}$), octacosane ($C_{28}H_{58}$) and nonacosane ($C_{29}H_{60}$) (Table 2). The analysis of the sex pheromones from *P. praetexta* revealed only one peak at the retention time of 11.70 min., but it could not unidentified by using GC-MS standard libraries (Figure 2, c) and Table 2). Nonetheless, we were unable to detect any chemical compounds from the sex pheromones of the female *L. tenebrosa* (Figure 2, d) and Table 2).

When compare the sex pheromones of each firefly species, only the chemical compositions from *Diaphanes* sp.1 and *Diaphanes* sp.2 were clarified (Table 2). Both species released six chemical compounds in their sex pheromones, in which four compounds were similar; i.e. tetracosane, pentacosane, hexacosane and heptacosane.

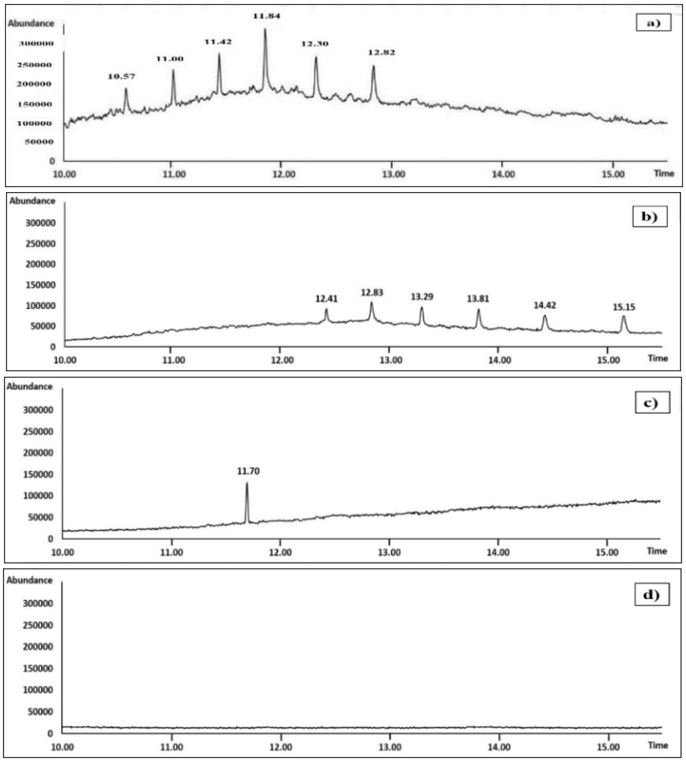

Figure 2 Total ion chromatogram (TIC) of the volatile components of the fireflis sex pheromones, a) *Diaphanes* sp.1, b) *Diaphanes* sp.2, c) *P. praetexta*, and d) *L. tenebrosa*.

Table 2 Chemical composition of sex pheromones of *Diaphanes* sp. 1, *Diaphanes* sp. 2, *P. praetexta* and *L. tenebrosa* as determined by GC-MS.

ID No.	Compounds	Retention time (min)			
		Diaphanes sp.1	*Diaphanes* sp.2	*P. praetexta*	*L. tenebrosa*
1	Docosane ($C_{22}H_{46}$)	0.57	n.d.	n.d.	n.d.
2	Tricosane ($C_{23}H_{48}$)	11.00	n.d.	n.d.	n.d.
3	Tetracosane ($C_{24}H_{50}$)	11.42	12.41	n.d.	n.d.
4	Pentacosane ($C_{25}H_{52}$)	11.84	12.83	n.d.	n.d.
5	Hexacosane ($C_{26}H_{54}$)	12.30	13.29	n.d.	n.d.
6	Heptacosane ($C_{27}H_{56}$)	12.82	13.82	n.d.	n.d.
7	Octacosane ($C_{28}H_{58}$)	n.d.	14.43	n.d.	n.d.
8	Nonacosane ($C_{29}H_{60}$)	n.d.	15.16	n.d.	n.d.
9	Unidentified	n.d.	n.d.	11.70	n.d.

n.d. = not detected

Hydrocarbons are organic compounds which are typically found in several insect pheromones, for example (Z)-9-tricosene and tricosane which found in sex pheromone of firefly species *P. oshimana* (Shibue et al., 2000), pentacosane in the sex pheromone of long-horned beetles, *Xylotrechus colonus* (Ginzel et al., 2003) and docosane, tetracosane, hexacosane, heptacosane, octacosane and nonacosane in the sex pheromone of the aphid species *Diuraphis noxia* (Bergman et al., 1990). From these reports, we may realize that tetracosane, pentacosane, hexacosane and heptacosane are common hydrocarbon compounds found in many insect sex pheromones. However, sex pheromone in some insects many contain other groups of chemical apart of hydrocarbons. For example, the detection of the male sex pheromone of giant danaine butterfly, *Idea leuconoe* consisted of a complex mixture of volatiles such as alkaloid derivatives, aromatic, terpenoids and hydrocarbons (Nishida et al., 1996).

The research of Stranger-Hall et al. (2007) reported that glow-worm fireflies use continuous light combined with sex pheromones for sexual communication. Our results showed the differences in the chemical composition of the sex pheromone of *Diaphanes* sp.1, *Diaphanes* sp.2 and *P. praetexta*. Therefore, it supported the theory that pheromones released from female fireflies to attract males are the main signals that glow-worm fireflies use to identify and recognize their mates (Lloyd, 1971; 1997). The species-specific pheromones in each species act as natural reproductive isolating mechanisms (West-Eberhard, 1984). Observation of *P. pectoralis* in Hubei province, China by Wang et al. (2007) revealed that during the courtship orientation flight, males search for females by producing a yellow-green glow. The glow acts as advertising visual signal of males, at the same time females sit on the ground and release glow light to indicate their presence. After locating a mate, females in response, release a sex pheromone to attract males. When the male detects chemical signals from the female, he reacts by quickly move the antennae and move lower to the ground to search for releaser. So that it can be assumed that, the glow-worm fireflies use continuous light as long-distance communication and chemical signal for short distant attraction. This pattern of courtship process was reported in *P. rufa* (Ohba, 2004) and this study. Sex pheromones act as mating signals occurred in all glowing fireflies but were absent in all fireflies that perform flashing (Ohba, 2004; Stranger-Hall et al., 2007). The reason that flashing fireflies do not release chemical sexual signals is that flashing fireflies use different light signals as interactive visual signals for species-specific recognition. This visual signal is used to distinguish the sex of the producer (Lloyd, 1966). Therefore, only a specific flash signal is needed to locate a mate of the same species. In contrast, those produce continuous glowing light without other signals, such as flash or chemical, there are not clear that which means an individual use to distinguish between its own and other species. Hence, other effective means must be employed as a species-specific mating signal. The emission of a bright glow was claimed as an intra-mediate evolutionary route between glow to flash. These patterns were reported in the genus *Pyractomena* and the species *Phausis reticulata* (Lloyd, 1997). As we reported here that no chemical components were detected from the firefly *L. tenebrosa* and they emit the very bright glow (Table 1 and Figure 1). The bright luminescence combines with large compound eyes and the absence of chemical released during mating encounters may indicate the evolutionary intermediate of this species to evolve from primitive glowing to flashing fireflies in the more advanced subfamily; Luciolinae.

CONCLUSIONS

The sympatric species of fireflies in the subfamily Lampyrinae share the characteristic of continuous luminescence. According to the fact that they might use other clues for discrimination among species, chemical signals seem to be a suitable choice for these fireflies. We detected chemicals from female released pheromones using GC-MS analysis and found significant compositions from each firefly species. The composition analysis detected six chemicals which are belonging to a class of hydrocarbon group from the female pheromones of *Diaphanes* sp.1 containing carbon 22 – 27 atoms which were docosane ($C_{22}H_{46}$), tricosane ($C_{23}H_{48}$), tetracosane ($C_{24}H_{50}$), pentacosane ($C_{25}H_{52}$), hexacosane ($C_{26}H_{54}$) and heptacosane ($C_{27}H_{56}$). Meanwhile, six chemicals from *Diaphanes* sp.2 possess carbon 24 – 29 atoms consisting of tetracosane ($C_{24}H_{50}$), pentacosane ($C_{25}H_{52}$), hexacosane ($C_{26}H_{54}$), heptacosane ($C_{27}H_{56}$), octacosane ($C_{28}H_{58}$) and nonacosane ($C_{29}H_{60}$). It is obvious that four chemicals, tetracosane, pentacosane, hexacosane and heptacosane, occurred in sex pheromones of both species of the genus *Diaphanes*. However, docosane and tricosane were only found in *Diaphanes* sp.1 while octacosane and nonacosane were only detected from the *Diaphanes* sp.2. Hence, the commonly shared chemicals (tetracosane, pentacosane, hexacosane and heptacosane) might play a role as a specific chemical sex pheromone within the genus *Diaphanes*.

Simultaneously, docosane and tricosane were species-specific chemical sex pheromones of the *Diaphanes* sp.1 and octacosane and nonacosane involved in species-specific recognition of the *Diaphanes* sp.2. In contrast, only one chemical was detected from the sex pheromone of the *P. praetexta*, but this chemical was not matched with any standard libraries (Wiley 7 n.), therefore, it was concluded as unidentified chemical. However, further identification via other techniques, such as MS-MS might be helpful for the analysis of this unidentified chemical. No chemicals were detected from the sex pheromones of the *L. tenebrosa*, even though several replications of chemical analysis were taken for the determination. Therefore, we conclude that the *L. tenebrosa* does not release any chemical sex pheromones during their mating encounters. We hypothesize that the absence of sex pheromones and the evidence of bright glow in the *L. tenebrosa* including the characteristics of less developed antennae and large compound eyes, could be verified as an intra-mediate evolutionary pathway from primitive glowing to more advanced flashing in fireflies.

ACKNOWLEDGMENTS

This research was partially funded by Naresuan University to W.W. (Project No. R2558C022). We also thank the Department of Biology, Faculty of Science, Naresuan University for providing the facilities for the experiments.

REFERENCES

Bergman, D.K., Dillwith, J.W., Campbell, R.K. & Eikenbary R.D. (1990). Cuticular hydrocarbons of the Russian wheat aphid. **Southwestern Entomologist, 15**(2), 91 – 100.

Bergmann, J., Reyes-Garcia, L., Ballesteros, C., Cuevas, Y. & Curkovic, T. (2016). Identification of the female Sex Pheromone of the Leafroller *Proeulia triquetra* Obraztsov (Lepidoptera: Tortricidae). **Neotropical Entomology, 45**(4), 351-356.

Branham, M.A. & Wenzel, J.W. (2000). The evolution of bioluminescence in cantharoids (Coleoptera: Elateroidae). **Florida Entomologist, 84**, 565-586.

Branham, M.A. & Wenzel, J.W. (2003). The origin of photic behavior and the evolution of sexual communication in fireflies (Coleopter: Lampyridae). **Cladistics, 19**, 1-22.

Carlson, D.A., Mayer, M.S., Silhacek, D.L., James, J.D., Beroza, M. & Bierl, B.A. (1971). Sex Attractant Pheromone of the House Fly: Isolation, Identification and Synthesis. **Science, New Series, 174**(4004), 76-78.

De Cock, R., & Matthysen, E. (2005). Sexual communication by pheromones in a firefly, *Phosphaenus hemipterus* (Coleoptera: Lampyridae). **Animal Behavior, 70**(4), 807–818.

Ginzel, M.D., Blomquist, G.J., Millar, J.G. & Hanks L.M. (2003). Role of contact pheromones in mate recognition in *Xylotrechus colonus*. **Journal of Chemical Ecology, 29**(3), 533 – 545.

Herrera, H., Barros-Parada, W., Flores, M.F., Francke, W., Fuentes-Contreras, E., Rodriguez, M., Santis, F. & Zarbin, P.H.G. (2016). Identification of a Novel Moth Sex Pheromone Component from *Chilecomadia valdiviana*. **Journal of Chemical Ecology, 42**, 908–918.

Jeng, M.L. (2008). **Comprehensive phylogenetics, systematics, and evolution of neoteny of Lampyridae (Insecta: Coleoptera)**. (Doctoral dissertation). University of Kansas, Lawrence, Kansas.

Lewis, S. & Cratsley, C. (2008). Flash signal evolution, mate choice and predation in fireflies. **Annual Review of Entomology, 53**, 293-321.

Lloyd, J.E. (1966). Studies on the flash communication system in *Photinus* fireflies. **University of Michigan Miscellaneous Publications, 130**, 1-95.

Lloyd, J.E. (1971). Bioluminescent communication in insects. **Annual Review of Entomology, 16**, 97–122.

Lloyd, J.E. (1997). Firefly mating ecology, selection and evolution. In Choe, J.C., Crespi, B.J. (Eds.). **Evolution of Mating Systems in Insects and Arachnids** (pp. 184-192). London: Cambridge University Press.

McDermott, F.A. (1966). **Lampyridae Pars. 9**. In Junk Schenkling (Ed.Sec.). Coleopterorum Catalogus, 1–149.

Nak-eiam, S. (2015). **Taxonomy and species distribution (Coleoptera; Lampyridae) in the North of Thailand**. (Doctoral dissertation). Naresuan University, Phitsanulok.

Nishida, R., Schulz, S., Kim, C.S., Fukami, H., Kuwahara, Y., Honda, K. & Hayashi, N. (1996). Male sex pheromone of a giant danaine butterfly, *Idea leuconoe*. **Journal of Chemical Ecology**, **22**, 949–972.

Ohba, N. (2004). Flash Communication systems of Japanese fireflies. **Integrative and Comparative Biology, 44**(3), 225– 233.

Phanmuangma, W. & Wattanachaiyingcharoen, W. (2017). Intraspecific communication patterns and evolutionary relationship of fireflies in subfamily Lampyrinae found in Northern of Thailand. **Proceedings of the 1st Suan Sunandha Academic National Conference on Science and Technology** (pp. 1938-1952). Bangkok: Suan Sunandha Rajabhat University.

Shibue, K., Goto, Y., Shibue, T. & Ohba, N. (2000). Analysis of sex-attractant pheromones of firefly *Pyrocoelia oshimana* by gas chromatography mass spectrometry. **Analytical Sciences, 16**, 995-996.

Stanger-Hall, K.F., Lloyd, J.E. & Hillis, D.M. (2007). Phylogeny of North American fireflies (Coleoptera: Lampyridae): Implications for the evolution of light signals. **Molecular Phylogenetics and Evolution, 45**, 33–49.

Van der Goes van Naters, W. & Carlson J.R. (2006). Insects as chemosensors of humans and crops. **Nature, 444**, 302-307.

Wang, Y., Fu, X., Lei, C., Jeng, M. & Nobuyoshi, O. (2007). Biological characteristics of the terrestrial firefly *Pyrocoelia pectoralis* (Coleoptera: Lampyridae). **The Coleopterists Bulletin, 61**(1), 85-93.

West-Eberhard, M.J. (1984). Sexual selection, competitive communication and species-specific signals in insects. In Lewis, T. (Ed.) **Insect communication** (pp. 283-324). London: Academic Press.