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黑翅螢之生物學與保育研究

The biology and conservation of the black-winged firefly, *Luciola cerata* Olivier (Coleoptera: Lampyridae)

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The biology and conservation of the black-winged firefly,

Luciola cerata Olivier (Coleoptera: Lampyridae)

本論文係吳加雄君(D92632002)在國立臺灣大學昆蟲學研究所完成之博士學位論文，於民國 99 年 09 月 17 日承下列考試委員審查通過及口試及格，特此證明

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中文摘要

保育生物學為一整合性科學，涵蓋自然、社會及人文科學之研究成果，以應用於保育策略之制訂與執行。黑翅螢(*Luciola cerata* Olivier)為臺灣特有種，在臺灣除台東、墾丁地區外，廣泛分佈於海拔 1500 公尺以下無光害污染之平地與山區，為臺灣賞螢季節之主要觀賞物種之一。本研究包含三個生物學研究，黑翅螢之形態、不同地區黑翅螢閃光模式之差異、黑翅螢雄蟲之二形性對於性擇之影響及一項社會科學研究—阿里山地區螢火蟲生態產業產值調查，共四個不同研究主題已做為日後制定黑翅螢之保育策略之基礎。黑翅螢屬中型螢火蟲，其溝通系統為 HP 系統，即雌蟲回應雄蟲閃光之閃光持續時間極為固定，約 0.07~0.09 秒。在臺灣中部之 4 月份，雄蟲夜間之閃光活動時間可區分為三階段，第一階段從 18:40~19:01，為暖身期；第二階段為活動期，由 19:02~21:39；最後階段為休息期，由 21:40~23:39；各階段雄蟲之閃光持續時間、閃光間隔時間及雄蟲數量皆有不同，而雄蟲飛行及爬行之閃光模式，可能為雄蟲之間相互競爭的方式。黑翅螢雄蟲具二形性，可依第二發光節之外形，區分成五角形及半橢圓形雄蟲，在不同性比之室內試驗中，在雄蟲比例較高時，雌蟲偏好與五角形雄蟲交尾；相較於與半橢圓形雄蟲交尾之雌蟲，與五角形雄蟲交尾者，能產下更多的卵，但當雌蟲比例較高時，雌蟲雖仍偏好與五角型雄蟲交尾，但對於半橢圓形雄蟲之雌蟲閃光回應時間則減少。本研究另於 2007 年 6 月至 2008 年 2 月止，以問卷成功訪問了 31 家賞螢活動興盛之阿里山地區民宿業者，結果得知業者經營賞螢活動平均 7.5 年，以春、夏季為主；導覽解說賞螢時段在 18:00~21:00 間，每晚一場；並推估阿里山地區民宿活動年營收約為 9 億 3 仟 1 百萬元。賞螢季 (4 月至 6 月) 業者總營收約 52,654,560 元，約占全年營收之 28.67%；非賞螢季 (7 月至次年 3 月)業者總營收 131,011,920 元，約占全年營收之 71.33%；賞螢季的月營收約 17,551,520 元 (54%)，顯著高於非賞螢季之月營收 14,556,880 元 (46%)，證實賞螢活動對於民宿及旅行業者所帶來的收益甚高。本研究最後建議：良好規劃之賞螢活動及持續的螢火蟲生態教育，是保育黑翅螢之較佳方式；但賞螢活動需有足夠之解說人員，以免少數遊客捕捉螢火蟲造成干擾；而賞螢活動所創造之利益亦需部分回歸社區，方能促使當地社區居民有意願持續投入螢火蟲之保育工作。

關鍵詞：黑翅螢、雄蟲二形性、生物發光、性擇、螢火蟲、生態產業

Abstract

Conservation biology is an integrated science, the studying results of nature, applying, social and humane science could be used in the management of conservation strategies. The black winged firefly, *Luciola cetata* Olivier is endemic to Taiwan, and also the main watching species in firefly-watching season. It is wide-separated firefly species under altitude of 1500 meter beside Taitung and Kenting area. It is the most abundant in the unlit mountain area. The topics of this study are three biological studying and one social science studying; these are the studying of morphology, the bioluminescence of *L. cerata* within a night, the dimorphism and sexual selection of male *L.cerata* and the out value of firefly eco-industry in Mt. Ali area. The results of these studies could become the basic of the conservation strategy for *L. cerata*., *L. cerata* is middle firefly, the communication system are HP system, it means that the female response delay time was fix, about 0.07~0.09 sec. The flashing behavior of male *L. cerata* could devided to three stages. The first stage is warm-up stage, 18: 40~ 19:01, then the active stage, 19:02~21:39; the last one is resting stage, 21:40~23:39. The time of flashing duration, interval and male numbers in each stage are different. The male *L. cerata* has dimorphism, pentagonal and semi-oval male upon the sharp of the 2^{nd} light segment. In the laboratory experiment with different sex ratios, when the male ratio were high, female preferred mating with pentagonal male and laid more eggs than the female matted with semi-oval male. Female still preferred mating with pentagonal male in relative high female ratio, the female response delay to semi-oval male was decreased. The income of the guesthouse manager and firefly watching tour operators in the Mt. Ali area was collected by questionnaire from Jun, 2007 to Feb, 2008. The data from 31 operators were collected. The average operators were 7.5 years. Tours were mainly conducted mainly during the spring and summer months. Firefly watching tours were conducted between 6-9:00 p.m., lasted about 1 hour, and the guesthouse guests were given one free tour per evening. The total travel business income in the Mt. Ali area amounted to NTD 931,000,000 annually. The annual income of the guesthouse manager during the firefly watching season (from Apr. to Jun.) and the rest of the year were NTD 52,654,560 dollars (28.67%) and NTD 131,011,920 dollars (71.33%), respectively. The monthly incomes during the firefly watching period and the non-firefly watching months were NTD 17,551,520 and NTD 14,556,880 respectively, which was a significant difference (p = 0.023, $\delta < 0.05$). The results show that firefly watching in the Mt. Ali area is beneficial to the guesthouse manager. This study suggests that a limited firefly-watching activity, well-planning firefly-watching season project and the continuing firefly ecological education are relative suitable methods for the conservation of *L. cerata*.

Keyword: *Luciola cerata*, male dimorphism, bioluminescence, sexual selection, firefly, eco-industry

General introduction

Conservation biology is an integrated science, so the study results of nature science, applying science and social science could be used in species conservation strategy in direct or indirect ways.

The conservation biology of fireflies is belonging to nature science or applying science. Fireflies are among the most characteristic of all insects, their spectacular courtship displays have inspired poets and scientists alike. With more than 2000 species in 100 genera, worldwide lampyrid bioliversity is impressive and includes diurnally active as well as nocturnal species. (Lloyd, 1978, 2002; Ohba, 2004; Viviani, 2002).

Over the past 50 years, we have gained considerable insight into the biology of lampyrid and their application. For application, the gene of *Photinus pyralis*'s luciferase was used for reporter gene and applied in the research of medicien (Ardehali *et al*., 1995), pathology of AIDS (Bernier *et al*., 1998), neurophysiology (Ahmed *et al*., 2000), pharmacy (Jin *et al*., 2000), virology (Barco *et al*., 2000); For the biology of lampyrid included the lampyrid signal systems (Lloyd, 1966), their mating ecology, and their predator-prey interactions, lampyrid phylogeny, the discovery of firefly nuptial gifts and new evidence that female choose their mates on the basis of male flash behavior, these studies also had numerous documents. The other studies of lampyrid were the biochemical mechanisms behind firefly bioluminescence and flash control and the relationship between firefly chemical defenses and predation.

The Taiwan firefly studies could be divided to several stages. In the beginning of 20^{th} century, Olivier and Pic recorded most of Taiwan firefly species (Olivier 1910, 1911a, b, 1913., Pic, 1911a, b, c, 1916,1917, 1918, 1944). In Japan-occupied period, Matsumura (1918, 1928) recorded another four species of Taiwan fireflies. From 1940s to 1960s, the researches of Taiwan firefly were absent. After middle of 1960s, some Japanese scholars made some field studies of Taiwan fireflies. By the middle 1990s, Taiwanese scholars began their studying for Taiwanese fireflies.

The studying results of Taiwanese scholars could be divided into several fields: systemic and phylogeny, fireflies resources surveying, lift cycle studying, the flashing behavior and the out value of firefly eco-industry.

Lai *et al*. (1998) reviewed the name list of Taiwan fireflies. Jeng and Yang (2003) and Jeng *et al*. (1998a, b, c, 1999a, b, 2000, 2001, 2002, 2003a, b, 2005, 2006a, b, 2007a, b) made numerous taxonomy and ecology studies of Lampyridae. Now, there are more than 50 lampyrid species in Taiwan, the firefly fauna in six national parks and some forests also have basic data for conservation management (Wu *et al*., 2008).

Though the results of most firefly resources surveying were published in popular science book (Ho and Chiang, 1997; Ho and Jong,1997; Yang, 1998; Ho *et al*., 2002; Chen,2003; Ho, 2007) and the life cycle studies are also abundant, the life cycle of some *Aquatica* and *Pyrocoelia* firefly were studied and some new techniques for artificial rearing have been developed (Chen *et al*., 1998; Ho, 1998; Ho and Chiang, 2002; Ho and Huang, 2003; Ho *et al*., 2003, Ho *et al*., 2010). Ohba and Yang (2003) was the first document to describe the communication system and flashing behavior of *Luciola cerata*. Wu *et al*. (2010) demonstrated the male dimorphism and mating behavior of *L. cerata*.

L. cerata was not protected wild animal and it was the main species for firefly-watching activities owing to their abundant number and bioluminescence (Ho *et al*. 2009). The topics of this thesis were focused on their flashing behavior, morphology and the economics studies, and a conservation strategy was offered based on the results of this study.

Chapter 1 was the morphological characters of *L. cerata*, chapter 2 and 3 were the flashing patterns in different area and their sexual selection.

Chapter 4 was the out value, current management situation of firefly eco-industry, and chapter 5 was the conservation strategy of *L. cerata*.

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Chapter 1

The morphological character of male and female *Luciola cerata* Olivier (Coleoptera: Lampyridae)

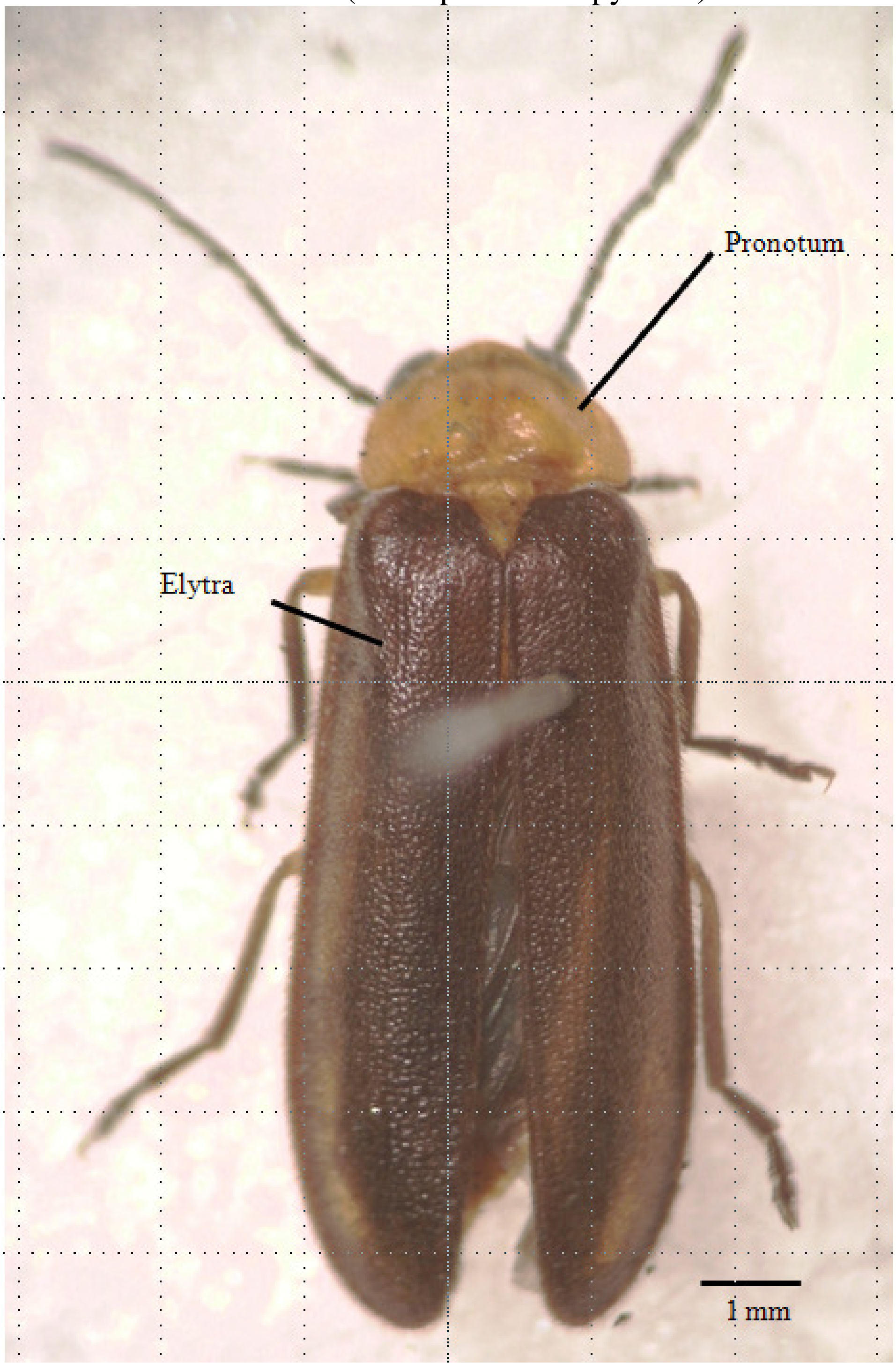

Fig. 1. The dorsal view of the male *Luciola cerata* Olivier.

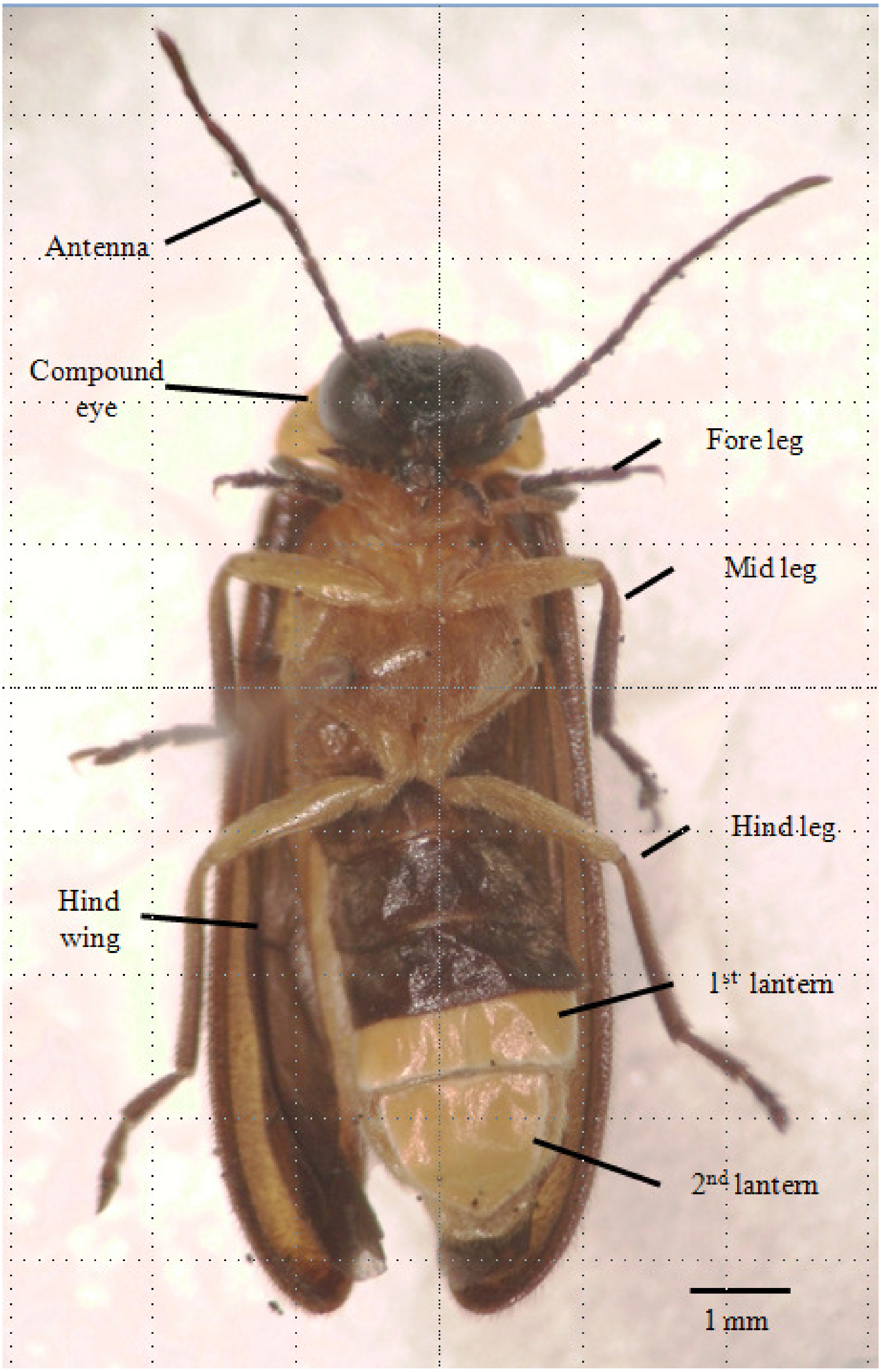

Fig. 2. The abdominal view of male *Luciola cerata* Olivier.

Fig. 3. The dorsal vies of female *Luciola cerrata* Olivier.

Fig. 4. The abdominal view of female *Luciola cerata* Olivier.

Chapter 2

Evidence for two male morphs exhibiting distinct mating behavior in *Luciola cerata* Olivier (Coleoptera: Lampyridae) with implications for sexual selection

Abstract

The black-winged firefly *Luciola cerata* Olivier is endemic to Taiwan and is the most common firefly on the island. *L. cerata* males flash spontaneously and females respond with bioluminescent flashes at fixed response delays. Prior studies of North American fireflies exhibiting a similar communication system have found intraspecific variation in male morphology and flash patterns along with evidence for female choice, male scramble competition, and male courtship investment in the form of spermatophores. In order to explore the potential for sexual selection in *L. cerata,* we surveyed males at 12 sites in Taiwan. We measured variation in male morphological characteristics and mated males to females, weighting them before and after mating to assess the potential for spermatophore transfer. Male flash behavior and mating success were quantified under a variety of experimental sex ratios in the lab. We found there are 2 male morphs of this species, which are distinguishable only by the morphology of the lantern. One morph has a pentagonal 2nd light segment, while the other has a semi-oval 2nd light segment and only produces a flash with first segment of the lantern segments. Besides this difference in morphology, the flash patterns and mating behavior also differ between these 2 types. Males with a pentagonal segment have a faster flashing rate than those with a semi-oval segment and are considered more attractive to females in groups with male-biased sex ratios. Further, females that mate with the former type demonstrated greater fecundity than those that mate with the latter type.

Key words: *Luciola cerata*, dimorphism, sexual selection, Lampyridae, firefly

Introduction

Mating behavior and the mechanisms of sexual selection vary greatly across many known species of fireflies. It has been predicted that much of this variation depends upon the status of nuptial gift production in each species, as females are apparently polyandrous when nuptial gifts provide material benefits (see Lewis and Cratsley *(*2008*)* for review). Such nuptial gifts have the ability to potentially increase a female's lifetime fecundity, thereby resulting in selection for both polyandry and post-copulatory female choice (Boggs 1995, Vahed 1998, Gwynne 2008). Lewis and Wang (1991) found that *Photinus aquilonius* and *P. marginellus* are polygamous, mating behavior appears to be affected by predictable seasonal shifts in operational sex ratios, such that male-male competition and female choice prevail early in the flight season, while interfemale competition and male selectivity may predominate later in the season.

Photinus collustrans is another example. They are largely monogamous lacking the ability to produce nuptial gifts, and males seek wingless females at twilight. Females remain mostly motionless, signaling to males flying above. Once mating is complete, the females return to their underground burrows (Wing, 1984, 1988, 1989, 1991). Branham and Greenfield (1996) demonstrated that female *P. consimilis* do not simply emit signals of a high photic power; they prefer flash rates that exceed the mean rate in the male population and flash lengths that approximate the mean. *P. pyralis* is another example of how sex ratios affect mating behavior and sexual selection. In populations with a low male density, females prefer large males, but as male-male competition increases, small males have an opportunity to mate because they move faster than large males (Vencl and Carlson, 1998).

Courtship behaviors in many *Luciola* fireflies consist of short bioluminescent flashes but are considerably complex and highly varied (Lloyd, 1972, 1973, 1974; Ohba, 2004a, 2004b; Papi, 1969). For example, in the case of *L. cruciata*, males flash synchronously while in flight (Ohba, 1984, 2004b). The females flash spontaneously as well as in response to male signals. Flying males are attracted to flashing females, land nearby, and display diverse flashing behaviors before contact and copulation occur.

Reports of the bioluminescent signaling behaviors of Taiwan's *Luciola* fireflies are quite scarce, and these behaviors remain understudied. Ohba and Yang (2003) reported on the bioluminescent behavior and communication system of the black-winged firefly *L. cerata* in the field. The communication system is classified to be of the HP variety, which means that the female responds to the male at fixed intervals. The average of flash interval of flying males was 0.69 to 0.85 sec at different census sites. The interaction of male and female was also recorded. The results of Ohba and Yang (2003) were the first document about L. *cerata*'s mating biology, but the details of the mating system of *L. cerata* are still unknown. In this study, we observe the courtship interactions between males and females of this firefly as a function of different sex ratios. Female behavior and subsequent fecundity in different groups were also recorded. We also demonstrate the existence of 2 distinct male morphs that exhibit 2 types of mating strategies, a phenomenon that has not been documented in any other lampyrid species to date.

Materials and Methods

Luciola cerata Olivier, 1911

L. cerata is a firefly species endemic to Taiwan (Lai *et al*., 1998), with a wide distribution from regions at sea level to an elevation of 1500 meters (Jeng *et al*., 1999). Like many firefly species, this species has a sexually dimorphic lantern; the lantern in males has 2 segments capable of producing the characteristic bioluminescent flash. Males also have relatively large compound eyes and a relatively small body size.

Females, on the other hand, have a single-segment lantern, smaller compound eyes, and a relatively large body size. Adults emerge in March and remain until May. During this period, they can be found in various habitats, including densely vegetated sloping fields, forest trails, and unlit roads. Many of their habitats are characterized by high humidity, and they are especially abundant in areas lacking light pollution.

Morphological characteristics of male *L. cerata*: fresh individuals and dry specimens

77 fresh males *L. cerata* was frozen in -20℃ refrigerator for 30mins, the shape and size (length and width) of the 2nd light segment and the body length, width, and weight of them were determined with a stereomicroscope (Leica, MZ16) and electric balance (AND ER-120A) in the year 2008. For some morphological characters of male *L. cerata* didn't measured in year 2008. The body length and width, head width, protergum width, and elytra length and size (length and width) were measured for the dry specimens of another 29 male *L. cerata* individuals in the year 2009.

Effect of mating on body weight and female fecundity of lab reared and field-caught *L. cerata*

16 pairs (13 males with pentagonal 2nd light segments [henceforth referred to simply as pentagonal males], 3 males with semi-oval 2nd light segments [henceforth referred to as semi-oval males], and 16 females) of lab-reared *L. cerata* individuals were used. We paired one lab-reared male and one lab-reared female in the round transparent plastic box (height: 8 cm; diameter: 10 cm) for mat. The body weight of them was measured using an electric balance (AND ER-120A) before and after copulation. The same was done for another 10 pairs (2 pentagonal and 8 semi-oval males and 10 females)

of field-caught *L. cerata* individuals. After copulation, every single mated female was placed in another round transparent plastic box (height: 8 cm; diameter: 10 cm) with 40 mm by 40 mm by 2 mm sponge for egg-laying until she died. The female fecundity, numbers of eggs in the sponge, was determined by visual counting with a stereomicroscope (Leica, MZ16).

The change of male and female weight ratio after mating were calculated as:

（(The weight after mating)- (The weight before mating)/ (the weight before mating)）x 100%.

Mating behaviors of and interactions between lab-reared male and female *L. cerata* individuals in the laboratory

Virgin lab-reared males and females were individually placed in a round transparent plastic box (height: 8 cm; diameter: 10 cm), and their flashing behavior was recorded using a Sony TRV-30 camera. These observations of individuals visually isolated from any other fireflies and these individual observations served as a control for the subsequent experiments with altered sex ratios. To identify the different individuals, we used the color pen (SC-S-M, SUPER COLOR, PILOT, Made in Japan) to spot the elytra with small, differently colored dots.

In 2008, the interaction between males and females in groups exhibiting a male-biased (2 males, 2 males vs.1 female, 4 males vs. 1 female, 12 males vs. 1 female, 8 males vs. 3 females) or female-biased sex ratio (1 male vs. 2 females, 2 males vs. 3 females) was also recorded using the camera. The flash duration and flash interval in all control and experimental groups were measured in a frame-by-frame analysis conducted using Windows Movie Maker. Another 2 groups with female-biased sex ratios (2 males vs. 3 females and 5 males vs. 6 females) were utilized in the experiments conducted in 2009.

Ratio of the 2 types of males at different sites: Field census of *L. cerata* males

During the spring of 2006, 12 survey sites were visited: Tou-Cheng (121° 47′ 13″E, 24° 50′ 56″N; Ilan county), Pin-Shih (121° 44′ 2.4″E, 25° 1′ 31.9″N; Taipei county), Wu-Lai (121° 31′ 28.8″E, 24° 49′ 31.3″N; Taipei county), San-Xia (121° 27′ 08″E, 24° 50′ 09″N; Taipei county), Fu-Xing (121° 21′ 41″E, 24° 42′ 58″N; Taoyuan county), Bei-Pu (121° 03′ 53″E, 24° 40′ 21″N; Shizhu county), Shi-Tan (120° 55′ 10″E, 24° 31′ 22″N; Maioli county), San-Yi (120° 45′ 55 ″E, 24° 23′ 36″N, Maioli county), Tung-Shih (120° 50′ 41.7′E, 24° 16′ 35.8″N; Taichung country), Tung-San (120° 25′ 54″E, 23° 16′ 51″N; Tainan county), San-Min (120° 42′ 6.9″E, 23° 15′ 38.7′N; Kaohsiung county), and Rui-Sui (121° 21′ 15.5″E, 23° 35′ 18.8″N; Hualien county). *L. cerata* individuals were collected from all 12 sites (Fig. 1). These 12 survey sites were all sloping fields densely vegetated with shade-loving plants. Three sites were along forest trails (Wu-Lai, Rui-Sui, and Tung-Shih), and the other 9 sites were on unlit roads. We used sweeping net method to catch male *L. cerata* individuals from a square area of 5 m by 5 m area from 7:00 to 7:10 P.M. Other species could be distinguished by their flickering flashing patterns (e.g., *L. filiformis*) or light coloration (e.g., *L. kagiana*), and these fireflies were not caught during the census.

Statistical analysis

SYSTAT statistical software version 10.2 (Systat Software Inc.) was used to perform all statistical analyses. In the experiments testing for differences between male fireflies, one-way analysis of variance (ANOVA) was used.

Results

Morphological characteristics of male *L. cerata*: fresh individuals and dry specimens

Male *L. cerata* individuals exhibit dimorphism in terms of the shape of the 2nd flashing segment (Fig. 2). As judged using fresh specimens, pentagonal males have relatively larger body length, width, and weight, and 2nd flashing segment than semi-oval males. The results are similar for dry *L. cerata* specimens, but besides a difference in the 4 abovementioned parameters, pentagonal males also have a relatively greater protergum width and elytra length than semi-oval ones, although the difference in the head width and size of the 1st flashing segment is not statistically significant (Table 1).

Effect of mating on body weight and female fecundity of lab reared and field-caught *L. cerata*

After copulation, the body weight of males did not change significantly. By contrast, that of females increased substantially (Table 2). These females also exhibited relatively higher fecundity than those that mated with semi-oval males. These observations may be attributed to the transfer of larger spermatophores from pentagonal males to females during mating (Fig. 3).

Mating behaviors of and interactions between lab-reared male and female *L. cerata* individuals in the laboratory

In terms of the morphology of the 2nd light segment, 2 different morphs of male *L. cerata* are distinguishable, and they can be categorized as pentagonal and semi-oval (Fig. 2). The mating behaviors of these 2 types of male *L. cerata* were very different. The pentagonal males flashed with both flashing segments, while the semi-oval males flashed with first segment when they do not get disturbed. Females that mated with pentagonal males exhibited greater fecundity and demonstrated a greater increase in body weight after mating (potentially indicating the transfer of a larger spermatophore), although the change in body weight after mating was not significantly different between the 2 male morphs (Table 2). The change in the female body weight after mating could be attributed to the transfer of the male spermatophore (Fig. 3). Dissection of female individuals showed that the reproductive systems of females that had just copulated were similar to those of virgin females (Fig. 4).

In the individual observations, neither males nor females flashed, and both were motionless (they remained on the wall of the round box in which they were placed); however, in the experimental groups, the males crawled and engaged in flash dialogues with the females. In groups with 2 males of different types (1 pentagonal male and 1 semi-oval male), the pentagonal male crawled around the box, and its flash interval changed from 1.10 ± 0.25 sec (mean ± SE) to 9.92 ± 0.58 sec (Fig. 5). While the pentagonal male was flashing and crawling, the semi-oval male merely remained motionless on the wall and did not flash. After 10 min, the pentagonal male stopped flashing and also remained stationary on the wall like the semi-oval male.

In all the experiments, the flashing duration was about 0.16~0.19 sec in both types of males. Observations were recorded for a series of male-biased groups, with the following numbers of males and females: 2 males (1 pentagonal and 1 semi-oval) and 1 female, 4 males (2 pentagonal and 2 semi-oval) and 1 female, 12 males (7 pentagonal and 5 semi-oval) and 1 female, and 8 males (5 pentagonal and 3 semi-oval) and 3 females. The flashing interval of the males flashing with 1 flash segment (OFS) was 4.191~5.136 sec, and that of the males flashing with 2 flash segments (TFS) decreased (4.062~3.306 sec) when the number of males in the male-biased ratio increased (Table 3). When the ratio was female biased (1 pentagonal male and 2 females, 2 males (1 pentagonal and 1 semi-oval) and 3 females), the flashing intervals of the TFS and OFS males were 3.30~4.06 4.856 sec, respectively (Table 4).

In groups with a male-biased ratio, most females preferred mating with pentagonal males (N = 5), and only 1 female mated with an OFS male. In groups with a female-biased ratio, 5 females mated with TFS males, and only 2 females mated with OFS males. In the male-biased groups, the response delay time for females that mated with TFS and OFS males was 0.078~0.079 and 0.235 sec, respectively. The female response for OFS males was quicker in the female-biased groups than in the male-biased groups. It was 0.072~0.090 sec for females that mated with TFS males and 0.156 sec for females that mated with OFS males.

The time after which females initiated copulation was 2.6~4.0 min in the case of TFS males, which is shorter than that in the case of OFS males (26.0~65.0 min). In all experiments, the mating duration was 159.0~175.4 min in the case of TFS males, and 47.5~75.0 min in the case of OFS males (Table 3).

In the female-biased groups, some TFS males mated twice, and the mating duration was 160~166 min (Table 4.)

While a female and her chosen mate were engaged in dialogue, other males attempted to mate with her. These males would crawl to the female, mount her dorsally, and directly extend their genitalia without attempting any kind of flash communication with her. Invariably, the female would not accept these attempts at copulation and would instead only accept the attempts of the communicating male. Once copulation had begun, other males would still attempt to mount the female, but these attempts were unsuccessful. However, after copulation was completed, the unmated males did not attempt a second copulation with the female that had just mated. This might be attributed to the presence of the male’s spermatophore in the female’s reproductive tract.

In the male-biased groups, all the males mated only once, but in the female-biased groups, the pentagonal males mated multiple times. The females found a mate and began copulating quicker in the male-biased groups than in the female-biased groups, but in both groups, the females preferred to mate with pentagonal males than semi-oval ones.

Ratio of the 2 types of males at different sites: Field census of *L. cerata* males

There were many more pentagonal males than semi-oval ones (number of pentagonal males = 21.25 ± 3.47; number of semi-oval males = 7.83 ± 1.62), and the pentagonal/semi-oval male ratio was 3.39/1 in all sites expect SB (Table 5).

Discussion

Many nocturnally active fireflies use discrete pulses to locate their mates. In these species, males are the primary signalers (Lewis and Cratsley 2008). In *L. cerata*, although males are the primary signalers, male flashing behavior is significantly reduced in the absence of females.

L. cerata has an HP communication system (Ohba and Yang 2003), and one of the characteristics of this system is that the female response delay time is constant (Ohba 1983). The results of this study support this previous finding since a relatively small standard error was observed in the female response delay time (Table 3).

The mating behavior and mechanisms of sexual selection in *L. cerata* are similar to those in *P. pyralis*: large males have a better opportunity to mate, but small males still have a chance as mating competition increases (i.e., when the sex ratio is high). There are some differences in the male-male competition modes in these 2 firefly species. The male-male competition among large *P. pyralis* and *L. cerata* individuals is based on the ability to attract females through flashing behavior; the type of competition among small *P. pyralis* individuals is scramble competition (via mobility), but small *L. cerata* individuals have an alternative tactic (a type of contest) because semi-oval males flash with one light segment, thereby resembling a female in the field. Most *L. cerata* females prefer mating with pentagonal males, because of which the number of pentagonal males is much greater than that of semi-oval males in the field.

Because female *L. cerata* individuals mate are monogamous they prefer mating with pentagonal male *L. cerata* individuals, which appear to have relatively larger spermatophores. Thus, the females who mate with the pentagonal males exhibit relatively greater fecundity. This result is consistent with previous studies examining the fitness effects of spermatophores on female firefly fecundity. Rooney and Lewis (2002) documented a relative fecundity increase of 73% in triply vs singly mated female *P. ignitus* fireflies. Thus, this study contributes to the growing body of literature of fitness benefits of spermatophores in worldwide firefly species. Females also lay more eggs when the sex ratio is male biased, perhaps because they have greater choice of males, and they can choose the one capable of producing lager spermatophore. Females that mate with semi-oval males or with pentagonal males mating for the second time lay less eggs, probably because they have less choice in a female-biased group or receive a relatively smaller spermatophore from the first mating with the semi-oval male.

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Table 1. Comparison of body size, body weight, size of 1st segment, size of 2nd light segment, protergum length, and elytra length between the 2 types of male *Luciola cerata* Olivier.

	Fresh TFS (n = 46)	Fresh OFS (n = 31)	*P* value
Body length (mm)	9.12 ± 0.05[a]	8.73 ± 0.14[b]	0.014
Body width (mm)	3.01 ± 0.01 [a]	2.86 ± 0.01 [b]	0.001
Weight (g)	0.024± 0.001 [a]	0.017 ± 0.001 [b]	0.001
Length/width of 2nd light segment	0.93 ± 0.01 [a]	0.67 ± 0.00 [b]	0.002
	Dry TFS specimen (n = 19)	**Dry OFS specimen (n = 10)**	***P* value**
Head width (mm)	1.76 ± 0.04 [a]	1.71 ± 0.07 [a]	0.226
Body width (mm)	3.56 ± 0.04 [a]	3.31 ± 0.01 [b]	0.015
Protergum width (mm)	2.53 ± 0.03 [a]	2.41 ± 0.01 [b]	0.035
Body length (mm)	8.97 ± 0.16 [a]	8.41 ± 0.22 [b]	0.044
Elytra length (mm)	0.72 ± 0.01 [a]	0.69 ± 0.01 [b]	0.040
Length/width of 1st flash segment	0.31 ± 0.01 [a]	0.30 ± 0.02 [a]	0.457
Length/width of 2nd flash segment	0.75 ± 0.02 [a]	0.65 ± 0.01 [b]	0.036

TFS: male with pentagonal segment flashing with both flash segments; OFS: male with semi-oval segment flashing with first flash segment

Table 2. Change in female body weight and fecundity as a function of the type of male *Luciola cerata* that the female mated with

	TFS (n = 15)	OFS (n = 11)	*P* value
Male weight ratio after mating (%)	–3.02 ± 0.01 [a]	–2.91 ± 0.04 [a]	0.66
Female weight ratio after mating (%)	+3.59 ± 0.50 [a]	+1.62 ± 0.50 [b]	0.04
Female fecundity (Number of eggs)	75.00 ± 1.81 [a]	50.25 ± 3.33 [b]	0.0002

Table 3. Flash duration (FD), flash interval (FI), female response delay time (FRDT), time of initiation of first copulation (TIFC), first mating duration (FMD) of TFS (male with pentagonal segment flashing with 2 flashing segments), OFS (male with semi-oval segment flashing with 1 flashing segment), and female (F) *Luciola cerata* Olivier in groups with male- biased ratios

	FD (sec)		FI (sec)		FRDT (sec)		TIFC (min)		FMD (min)	
Sex ratio	TFS	OFS	TFS	OFS	TFS	OFS	TFS	OFS	TFS	OFS
1 TFS 1 OFS	0.179 ± 0.011 (n = 1)		2.782 ± 0.879 (n = 1)							
1 TFS 1 OFS 1 F	0.181 ± 0.008 (n = 1)	0.171 ± 0.011 (n = 1)	4.062 ± 0.404 (n = 1)	4.999 ± 0.379 (n =1)	0.078 ± 0.005 (n = 1)		3.10 (n = 1)		166.50 (n = 1)	
2 TFS 2 OFS 1 F	0.187 ± 0.004 (n = 2)	0.164 ± 0.009 (n = 2)	3.755 ± 0.192 (n = 2)	5.136 ± 0.252 (n = 2)	0.078 ± 0.003 (n = 1)		4.40 (n = 1)		175.40 (n = 1)	
7 TFS 5 OFS 1 F	0.186 ± 0.002 (n = 7)	0.182 ± 0.003 (n = 5)	3.306 ± 0.067 (n = 7)	4.191 ± 0.143 (n = 5)	0.078 ± 0.001 (n = 1)		4.00 (n = 1)		168.50 (n = 1)	
5 TFS 3 OFS 3 F	0.189 ± 0.002 (n = 5)	0.181 ± 0.005 (n = 3)	3.415 ± 0.072 (n = 5)	4.289 ± 0.192 (n = 3)	0.079 ± 0.003 (n = 2)	0.235 ± 0.009 (n = 1)	3.90 ± 0.25 (n = 2)	65 (n = 1)	168.50 ± 0.15 (n = 2)	75 (n = 1)

Table 4. Flash duration (FD), flash interval (FI), female response delay time (FRDT), time of initiation of first copulation (TIFC), time of initiation of second copulation (TISC), first mating duration (FMD)and second mating duration (SMD) of TFS (male with pentagonal segment flashing with 2 flashing segments), OFS (male with semi-oval segment flashing with 1 flashing segment), and female (F) *Luciola cerata* Olivier in groups with female-biased ratios

	FD (sec)		FI (sec)		FRDT (sec)		TIFC (min)		FMD (min)		TISC (min)	SMD (min)
Sex ratio	TFS	OFS	TFS	OFS	TFS	OFS	TFS	OFS	TFS	OFS	TFS	TFS
1 TFS 2 F	0.181 ± 0.008 (n = 1)		4.062 ± 0.405 (n = 1)		0.079 ± 0.005 (n = 1)		2.60 (n = 1)		159 (n = 1)		7.9 (n = 1)	160.7 (n = 1)
2 TFS 2 OFS 6 F	0.180 ± 0.005 (n = 2)	0.198 ± 0.006 (n = 2)	4.067 ± 0.205 (n = 2)	4.856 ± 0.234 (n = 2)	0.090 ± 0.006 (n = 2)	0.156 ± 0.007 (n = 2)	2.70 ± 0.15 (n = 2)	26.00 ± 7.00 (n = 2)	166.50 ± 2.50 (n = 2)	47.5 ± 7.5 (n = 2)	5.2 ± 2.7 (n = 2)	166.3±3.3 (n = 2)
5 TFS 6 F	0.187 ± 0.002 (n = 5)		3.306 ± 0.067 (n = 5)		0.072 ± 0.001 (n = 5)		2.70 ± 0.08 (n = 5)		166.70 ± 7.20 (n = 5)		5.5 (n = 1)	165.0 (n = 1)

Table 5. Ratio of the 2 types of males in different survey sites.

Sampling site	Sample date (year/month/day)	Number of TFS males	Number of OFS males	Ratio (TFS/OFS)
HZ	2006/03/30	23	5	4.60
IT	2006/04/19	16	6	2.67
PP	2006/04/20	26	3	8.67
PS	2006/04/21	28	20	1.40
PW	2006/04/12	13	4	3.25
TF	2006/04/18	17	6	2.83
SB	2006/04/06	15	17	0.88
MST	2006/04/17	13	5	2.60
MSE	2006/04/16	25	6	4.17
CT	2006/04/15	53	11	4.82
NT	2006/04/25	11	6	1.83
HS	2006/03/21	15	5	3.00
Sum		255	94	
Average		21.25	7.83	3.39
Stand error		3.47	1.62	0.61

HZ: Hualien Rui-Sui; IT: Ilan Tou-Cheng; PP: Taipei Pin-Shih; PS: Taipei San-Xia; PW: Taipei Wu-Lai; TF: Taoyuan Fu-Xing; SB: Sinzhu Bei-Pu; MST: Maioli Shi-Tan; MSE: Maioli San-Yi; CT: Taichung Tung-Shih; NT: Tainan Tung-San; HS: Kaohsiung San-Min; TFS: male with pentagonal segment flashing with both flash segments; OFS: male with semi-oval segment flashing with first flash segment

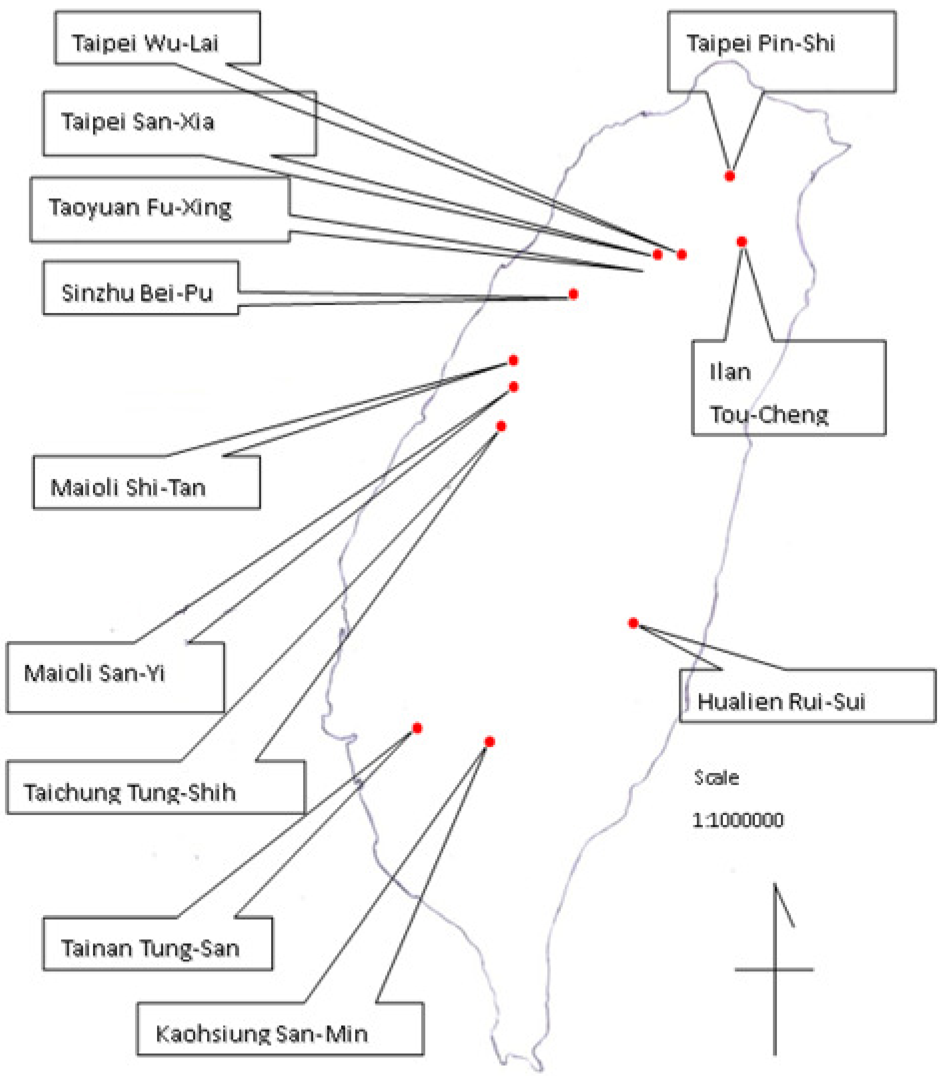

Fig. 1. Location of the 12 survey sites in Taiwan.

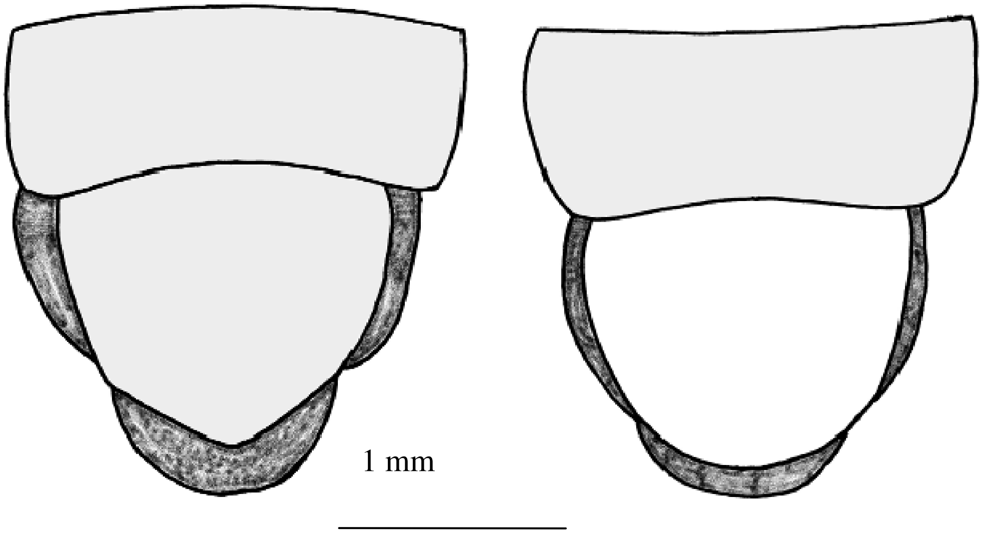

Fig. 2. Shape of the 2nd light segment in the 2 morphs of male *Luciola cerata* Olivier. In the one on the left, the last segment is pentagonal, while in the one on the right, it is semi-oval. The gray segments indicate those used to produce the bioluminescent flash in each morph.

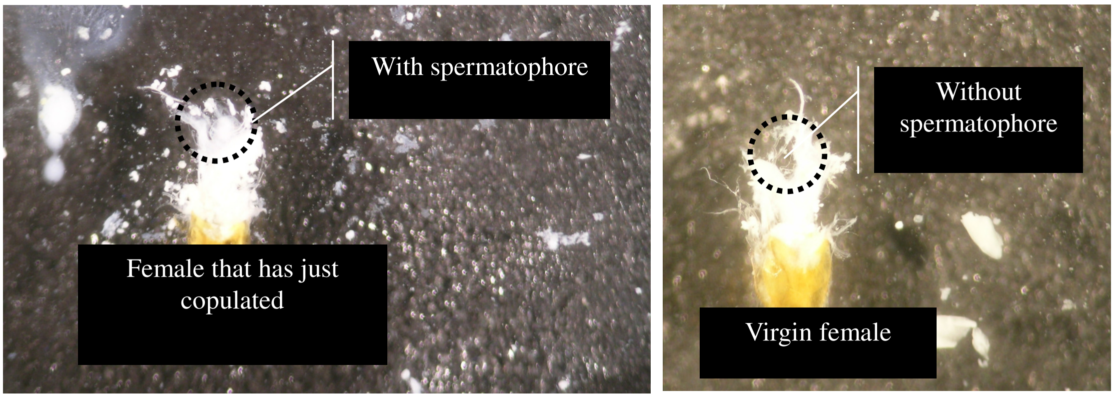

Fig. 3. Comparison of the vagina (right: virgin female; left: female that has just copulated); female obtains spermatophore (black dotted circle) after copulation.

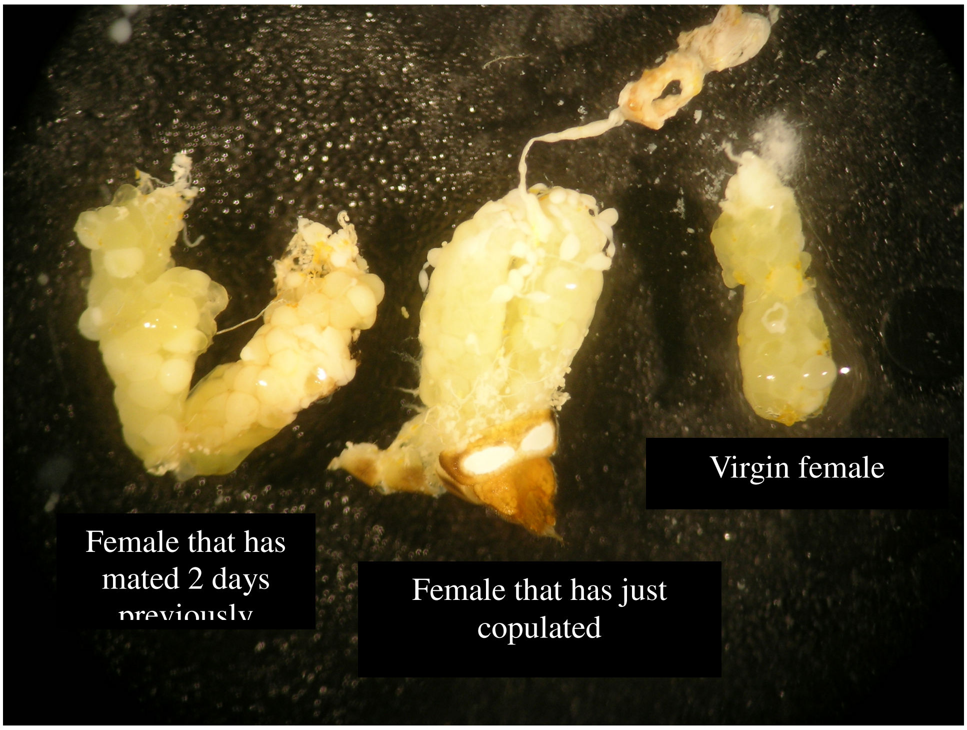

Fig. 4. Ovaries of mated (left), recently copulated (central), and virgin (right) females. The ovaries of the recently copulated female are similar those of the virgin female, so the increase the in female body weight after copulation could be attributed to the transfer of the male spermatophore.

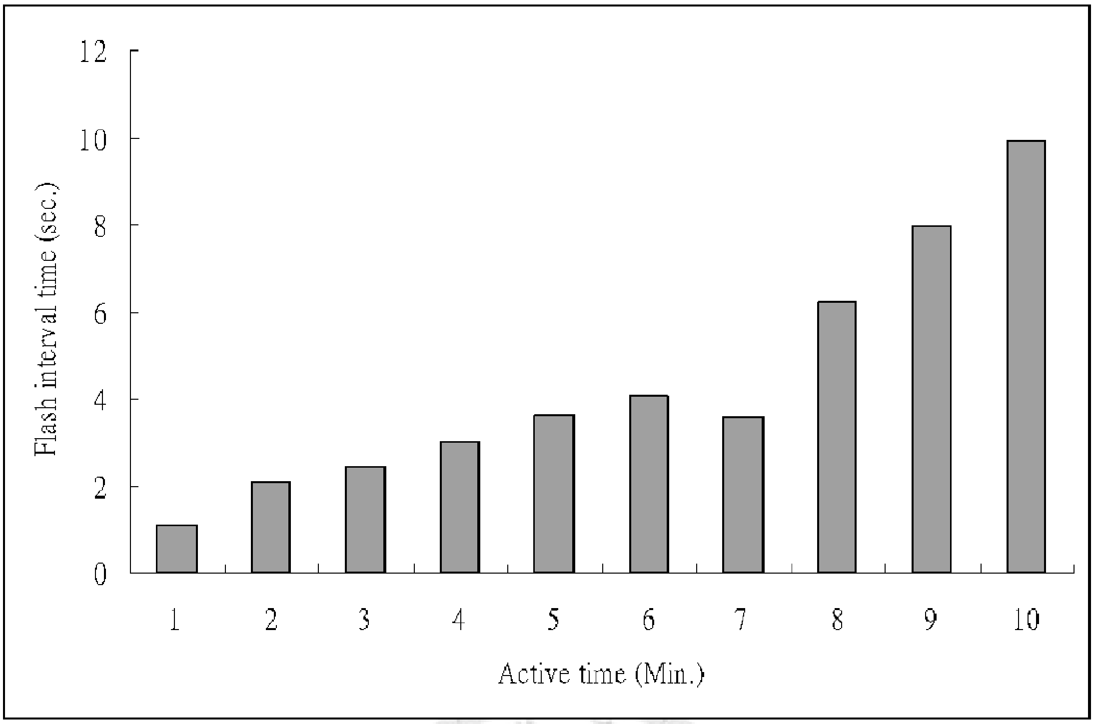

Fig. 5. Average flash interval of male *Luciola cerata* Olivier (pentagonal male) in groups containing both types of males. X axis = active time in minutes; Y axis = flash interval in seconds.

Chapter 3
Nightly and Seasonal Variations in Flash Patterns of *Luciola cerata* Fireflies (Coleoptera: Lampyridae) in Taiwan

Abstract

The flash patterns and their variations in *Luciola cerata* fireflies were studied. The nightly bioluminescent activity of the males, lasting about five hours after sunset, can be divided into warm-up (first 20 minutes), active (next 2.5 hours) and resting stages. Males emit single-pulse flash signals in different flash durations and rates throughout the night. In active stage when most males were in patrolling, the signals have significantly longer flash duration but shorter flash intervals than those of the others. The nightly changes of IFI exhibited a negative correspondence with local male abundance, whereas FD had a positive correspondence with male abundance in general, but the trend was weak. Similar variations in courtship signal were also found in a mating season. Averaged FD was longer and IFI shorter in the peak time than in early or late season. It is suggested that the nightly and seasonal dynamics of flash patterns in *L. cerata* may be related to intensity of mating competition.

KEY WORDS: Lampyridae; *Luciola cerata*; firefly; flash patterns; signal variation

Introduction

Adult fireflies employ two fundamental signal systems for courtship and mating. Daytime-active species rely mainly on air-borne chemical cues to attract or locate their mates, whereas nocturnal groups use bioluminescence as a primary or secondary signal for the same purpose (Lloyd, 1966, 1973, 1979; Buck and Buck, 1966, 1968, 1976; Ohba 1983, 2004a, b). Lloyd (1971) divided the light-oriented communication of lampyrids into two major types. Type I, represented by European glowworm *Lampyris nocticula*, is featured with stationary, light-broadcasting females emitting continuous glows to attract flying, weakly or non-luminescent males. In Type II, both sexes of adults use photic signals to advertise themselves in mate-searching, and some groups can make intersexual dialogue by their flash signals. Additionally there exist intermediate or much more complicated forms besides the two types (Lloyd, 1979, 1997). Species capable of making intersexual flash-dialogues are called flashing or true fireflies (Lloyd, 1979). Taxonomically they belong to the Old World Luciolinae as well as several taxa like Photurinae, *Photinus*, *Pyractomena*, and *Aspisoma* from the New World (Branham and Wenzel, 2003; Stanger-Hall *et al*. 2007). A further division of flashing communication was proposed by Ohba (1983, 2004b) who differentiated them into three systems, HP, LC, and LL, depending on time lag of female response and occurrence of nuptial dancing/chasing or not.

The flash signals of fireflies serve as cues for both species recognition and mate choice (Branham and Greenfield, 1996; Lewis *et al.* 2004a; Lewis and Cratsley, 2008). Flash patterns of species-recognition are usually stable and clearly different from those of the other species. For mate recognition, subtle intraspecific variation in flash signals, especially of males, may serve as an index of mate quality to females in terms of nuptial gifts, and is subject to sexual selection (Branham and Greenfield, 1996; Lewis *et al*,. 2004a, b; Michaelidis *et al.,* 2006; Lewis and Cratsley, 2008). The light signals are also under influence of several internal and external factors, such as physiological conditions, different activities, population dynamics, ambient environment and predation risk (Lloyd, 1979, 1997; Forrest and Eubanks, 1995, Ohba, 2001; Cratsley, 2004; Lewis *et al.*, 2004b; Woods *et al.*, 2007). For instance, flash signals of male *Photinus collustrans* showed variation owing to flying speed, altitude and duration (Lloyd, 1979). Males of a *Photuris versicolor*, increased flashing rate with their active time, and sometimes changed flash patterns nightly as well (Forrest and Eubanks, 1995). Higher temperatures usually result in higher flash rate (Ohba, 2000, 2004a; Michaelidis *et al.*, 2006). In addition, it is not uncommon to find differentiation in flash pattern among ecotypes or geographic populations of a given species, like the symbolic Japanese Genji Hotaru, *Luciola cruciata* (Ohba, 1983, 1997, 2000, 2001, 2004a; Tamura, *et al.*, 2005).

Some fifty species of lampyrids, including the so called Ototretinae, are known to the Taiwan fauna. All 12 *Luciola* (*sensu lato*) and some *Curtos* species of Luciolinae from the island and its islets are flashing fireflies. Their flash patterns have not been quantitatively studied until Ohba and Yang (2003) analyzed those of the black-winged firefly, *Luciola cerata*. In this paper we analyzed the flash characteristics of the same species, showing its nightly and seasonal changes associated with activities and population dynamics.

Materials and methods

The species studied

The black-winged firefly, *Luciola cerata* Olivier (Fig. 1), is endemic to Taiwan and probably the most common spring species in western part of the island (Chen, 1999, 2003; Ho and Chu, 2002). It is also a popular species for firefly-watching activities or ecoturisms in many localities. The adults appear from late February to early June and usually reach the peak of the population in April, depending on latitude and elevation of localities. In the mating season, hundreds to thousands or more of the adults fly in mass in ecotone between forests and open-fields or on thin forest floors in the night. The males usually fly low, about two meters or lower, slightly above ground vegetations; females are found more frequently staying on the ground or vegetation than flying.

The bioluminescent color of male *L. cerata* is yellow (λ_{max}= 581.58±4.61 nm, n=12, Wu, 2001). Except intersexual dialogue, the flashing behaviors of the males can be categorized into three modes: patrolling (flying), crawling, and motionless. Courtship signals were emitted in the first two modes. The male signals largely comprise single-pulse flashes and the intersexual communication was determined to be HP type (abbreviation for *Hotaria parvula*, the representative species of the communication type), i.e., female respond male's signal in a fixed time lag (Ohba and Yang, 2003).

Surveying sites and measurement of environmental parameters

The male bioluminescent activities of *L. cerata* in two localities, Dongshi (120° 52' E, 24° 17'N, Taichung County) and Pingxi (121° 44' E, 25° 02'N, Taipei County), were recorded by the senior author in the springs of 2004 and 2005, respectively. The landscapes were mostly mildly-sloping and covered with broad-leaved evergreen trees and shade-living plants. The studying site in Dongshi was a hiking trail in a secondary forest, whereas that in Pingxi was a roadway without streetlamp.

Air temperature and ambient light intensity when firefly started flashing was measured with an alcoholic thermometer and a light meter (LM-81LX, Lutron Electronic Enterprise Company), respectively. Time of sunset was following the U.S. navy website (mach.usno.navy.mil) by inputting the GPS coordinates of the surveying sites.

Recording and analysis of bioluminescent activities of L. cerata

(1) General description

The male activities of *L. cerata* in the night were recorded in the field from sunset to about midnight with a digital camcorder (SONY, CCD-TRV-75 or SONY TRV-30), with aids of an infra-red light (SONY, HVL-IRH) for night-vision mode. The DV files were then transferred (films per second (FPS) = 60) and saved in a computer hard disc for further analyses. A non-commercial software developed by the coauthors (C.-S. Ouyang and J.-A. Jiang) called Automatic Analyzing System for Behavior of Firefly Luminescence (AASBFL), and Microsoft Windows Moviemaker were applied to measure the parameters of flash patterns for single or multiple individuals, respectively. The former automatically extracted flash parameters from the film and showed them in an Excel format. Male flash signals of *L. cerata* were essentially composed of single pulse in a regular timing, as demonstrated by Ohba and Yang (2003). Accordingly we used the flash (= pulse) duration (FD) and interflash interval (IFI) to describe and compare flash patterns (Fig. 2). It should be noted that the interpulse interval (IPI) used by several authors (e.g. Lloyd, 1966; Lewis *et al.*, 2004b; Michaelidis *et al.*, 2006) is equal to the length of a flash phrase but not IFI in our definition.

(2) Nightly variations in male flash signals

The analysis was based on a recording made in Dongshi during the mating season. The sampling site covered an area of about 5X6 square meters of land. Each time the senior author traced and videotaped a single male entering the square until it left, then repeated the process for the next male. After three hours of recording when most fireflies ceased flying, a whole-view of the sampling square was videotaped. To estimate the nightly dynamics of the fireflies, a colleague from the team used a hand counter to count the number of flashing males appearing in the sampling square for every first 15 seconds per minute during the five-hour recording.

The program AASBFL was employed to analyze the flash parameters for single-male recordings, whereas Windows Moviemaker was applied to the film with multiple resting males. By doing this we would like to see if the flash pattern changes with time in a night and if there exists correlations between these changes and dynamics of flashing male abundance.

(3) Variations in flash signals during a mating season

Three and four recordings were made in Dongshi and Pingxi in 2004 and 2005, respectively. This enabled us to examine the dynamics of flash patterns in a mating season. The recording and analytic processes were identical with the above, except that it covered a smaller area in Pingxi (4X5 square meters) and the local male abundance was not counted.

Results

Male bioluminescent activities in a night

A thorough recording was made in Dongshi in April 11, 2004. The sunset was at 18:17 and it was a black moon night. The ambient light intensity when males started to flash was 0.2 lux in maximum, and the temperature ranged from 13 to 15°C.

The flashing activities of *L. cerata* males can be roughly divided into three stages according to their behaviors and abundance of active individuals (Table 1). Stage I (warm-up stage) covered the first 22 minutes of activities (18:40-19:01). In the onset the males were not very active, produced light on their perching vegetations and only a few took off from there and flied low. The density of flashing and flying males then gradually increased with time. About ten minutes later after the males started flashing, a first female appeared in the film, recognized by her different flash pattern from that of the males. In the following 2.5 hours (19:02 to 21:39, Stage II or active stage), most of the males were either in patrolling flight or crawling on vegetations to seek potential mates. The male density was considerably stable in this stage. After then, males stopped flying one by one, remained motionless on low vegetations or ground but kept flashing for another two hours (21:40-23:39, Stage III or resting stage). The flashes became sparser and sparser with time, and eventually died out except few after 23:40.

Nightly variations and changes of flash signals in Dongshi

FDs among different stages of a nightly activity differed significantly (one-way ANOVA: $F_{2,\,297} = 553.254$, $p < 0.001$). They were about the same in the warm-up and the resting stages ($p = 0.813$), but significantly longer in the active stage ($p < 0.001$). Differences in IFIs among stages were also significant (ANOVA: $F_{2,\,297} = 190.257$, $p < 0.001$). IFIs shortened from Stage I to II, then increased again in Stage III. IFIs between Stage I and III were different significantly at 0.05 but not at 0.01 level ($p = 0.023$); IFI in Stage II differed significantly that of the other stages ($p < 0.001$). In short, males emit flash signals in more rapid rate (= shorter IFI) and longer duration (= longer FD) in their most vigorous stage than in the other two.

We analyzed the parameters of flash signals together with the male abundance along time and found considerable correlation between them (Figs. 3-4). FD had a positive correspondence in general with the number of male individuals appearing in the square (Fig.3), but the trend was weak. In contrast, IFI show a well-corresponding, negative relationship with the male abundance (Fig.4). Both FD and IFI were considerably stable in the second stage when the male abundance remained constant. FD did not significantly changed when male abundance increased (Stage I) or declined (Stage III), but were much shorter than that in Stage II in average. IFI exhibited clearly opposite trends with the male dynamics, and had great variations in the first and third stages.

Variations and changes of flash signals during mating season

We accessed the signal variations among the three behavioral modes and compared their changes within a mating season. In our survey, *L. cerata* reached its population peak in mid April of 2004 in Dongshi, and late April of 2005 in Pingxi. FD in patrolling and crawling modes from Dongshi population was about the same in the early and late mating season, but significantly longer in the climax stage (Table 2); FD in motionless mode was not different throughout the mating season. IFI, on the other hand, showed greater variations among modes as well as in different time of mating season (Table 3). In principle, IFI was shortest in the population peak during a mating season. Similar changes in FD and IFI in courtship signals with minor differences existed in Pingxi population. IFI of motionless in Pingxi did not change significantly throughout the mating season.

Discussion

In the field observation, males of *L. cerata* usually stated their bioluminescent activities in dusk. At first they flied low above forest floor, usually less than 50 cm high, then increased their flying height until the sky is dark. Ohba and Yang (2003) reported similar phenomena and stated that *L. cerata* may begin flashing when the ambient environment was still light enough to naked eyes of human beings (1.38 lux). Males of another congeneric species, *L. praeusta* Olivier in Taiwan, initial their flight in median vegetations in a forest when the sky is dark, then move to tree canopies in the active stage. The ambient light intensity when they begin flashing is usually under 0.1 lux (Jeng and Chen, unpublished). Both *L. cerata* and *L. praeusta* emit yellow flash signals but are different in onset timing and spatial utilization. It has been suggested that the yellow light of flash signals is an adaptation for twilight fireflies to discriminate mate signals from background light in dusk (Lall *et al*., 1980). Our observation indicates that phylogenetic relationship and behavioral adaptations may be important to the color ecology of flash signals in *Luciola* fireflies (s. lato).

Ohba and Yang (2003) recorded activities of *L. cerata* fireflies during the active stage of the night in a late mating season, with air temperatures from 19 to 25℃. The averaged patrolling IFIs were usually between 0.6-0.8 sec. except in Alishan (Ruili) population which had averaged IFI of 0.9-1.2 sec. In comparing with Ohba and Yang (2003), the patrolling IFI is generally smaller in the present study (Table 1) but about the same with that of the Alishan population. It is unclear whether the differences are owing to temperatures or population adaptations. According to Ohba and Yang (2003), it appears that higher temperature would result in higher flashing rate for *L. cerata*.

The averaged patrolling IFI in Table 2 is much higher than that of Ohba and Yang (2003) because our data combined the flying activity in both warm-up and active stages.

Though studies on the flash patterns and intersexual communications in Asiatic Luciolinae have been extensively conducted during the past three decades (see Ohba 2004a), the knowledge on the signal dynamics is considerably limited. From the present study, it is clear that the male flash signals of *L. cerata* have a nightly as well as a seasonal change. We also found that there existed a correlation between the signal changes with the intensity of bioluminescent activities in a night and with the population dynamics in a mating season. Forrest and Eubanks (1995) revealed that males of *Photuris versicolor* also have nightly and seasonal variation in their signals. In contrast to *L. cerata*, there is no significant correlation between the flash patterns and local male density.

The factors causing flash pattern changes are probably different from species to species. Forrest and Eubanks (1995) inferred that the changes could be a tradeoff between energy cost and mate availability or owing to predation risk. Demary *et al*. (2006) found the presence of predacious *Photuris* fireflies may alter the courtship interaction of their *Photinus* prey. Woods *et al*. (2007) demonstrated that the energy required to generate flash signals was very minor in relation the total cost of a courtship, while predation risk by *Photuris* fireflies is a major cost on courtship signals of *Photinus* species. There are no *Photuris* fireflies in the Old World where *Luciola* species distributed. In *L. cerata*, both nightly and seasonal change in flash patterns show a similar trend: signaling with a longer flash duration and at a higher flashing rate in the activities or days when mating competition is intense. It implies that such courtship signals of males may be preferred by the females during the male-bias environment in the field. This is potentially supported by indoor experiments which revealed that female *L. cerata* showed clear preference to males emitting courtship signals in a faster rate (shorter IFI), but are less sensitive to the variation of FD (Wu *et al*., paper submitted). In *Photinus* fireflies, females of different species use either pulse duration or rate to choose their mate (Carlson *et al.*, 1976; Branham and Greenfield, 1996; Cratsley, 2000, Cratsley and Lewis, 2003; Michaelidis *et al.*, 2006). Some species prefer longer pulse duration while the others like faster or intermediate flashing rate. In *L. cerata*, male flashing rate may be the primary trait subject to sexual selection but this needs further confirmation by playback experiments.

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Table I. Nightly variations in flashing duration and interval (mean±SD) of male flash signals of *Luciola cerata* fireflies in Dongshi Township, central Taiwan[1].

stage	Time	flash duration mean±SD range (sec.)	flash interval sec., mean±SD range (sec.)	Abundance[2] mean±SD range (males/min)
1st stage (warm-up)	18:40~19:01 (22 minutes)	0.200±0.043[a3] 0.04-0.24	2.348±0.741[a] 1.40-3.50	6.681±0.663[a] 2-13
2nd stage (active)	19:02~21:39 (158 minutes)	0.379±0.068[b] 0.04-0.48	1.054±0.037[b] 0.90-1.20	14.070±0.687[b] 11-18
3rd stage (resting)	21:40~23:39 (120 minutes)	0.197±0.024[a] 0.04-0.24	2.089±0.692[a] 1.28-3.19	5.033±4.031[c] 0-14

1. According to a five-hour videotaping conducted in the night of April 11, 2004.
2. Number of males appearing in a square of 5X6 m^2 in the first 15 seconds per minute
3. Means in each column followed by the same letter are not significantly different at $p<0.01$. FDs and IFIs between warm-up and resting stages did not different significantly ($p = 0.813$ and 0.023, respectively).

Table II. Variations in flash duration of the male signals of *Luciola cerata* fireflies during a mating season

Site	Date (number of males videotaped)	Modes of motion		
		Flying	Crawling (sec, mean±SE)	Motionless
Dongshi	2004/04/03 (24)	0.18±0.03	0.17±0.02	0.18±0.03
	2004/04/11 (50)	0.28±0.04	0.20±0.05	0.17±0.03
	2004/04/25 (08)	0.18±0.03	0.17±0.03	0.15±0.06
Pingxi	2005/04/20 (14)	0.16±0.02	0.17±0.03	0.14±0.02
	2005/04/29 (29)	0.28±0.03	0.20±0.06	0.17±0.04
	2005/05/04 (27)	0.17±0.02	0.19±0.04	0.15±0.02
	2005/05/10 (15)	0.15±0.03	0.16±0.03	0.16±0.04

Table III. Variations in interflash interval of the male signals of *Luciola cerata* fireflies during a mating season

Site	Date (number of males videotaped)	Modes of motion (sec, mean±SE)		
		Flying	Crawling	Motionless
Dongshi	2004/04/03 (24)	3.11±0.13	2.43±0.16	2.11±0.07
	2004/04/11 (50)	2.58±0.82	0.91±0.12	1.41±0.13
	2004/04/25 (08)	4.78±2.64	3.93±1.93	1.89±0.23
Pingxi	2005/04/20 (14)	3.85±2.03	3.56±2.04	1.91±0.34
	2005/04/29 (29)	2.58±0.92	0.91±0.12	1.85±0.13
	2005/05/04 (27)	2.73±1.22	1.05±0.12	1.59±0.13
	2005/05/10 (15)	4.61±2.01	3.23±1.98	1.86±0.27

Fig. 1. The trace of flash signals by *Luciola cerata* fireflies in flight in Dongshi Forest Area, Taiwan. The species is arguably the most abundant fireflies in the west part of Taiwan and an important resource of firefly-watching ecoturism in spring.

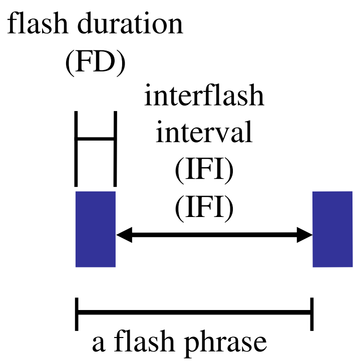

Fig. 2. Terminology of signal parameters in males of *Luciola cerata* fireflies used in this study. The length of a flash phrase is equal to the sum of a flash duration and an interflash interval.

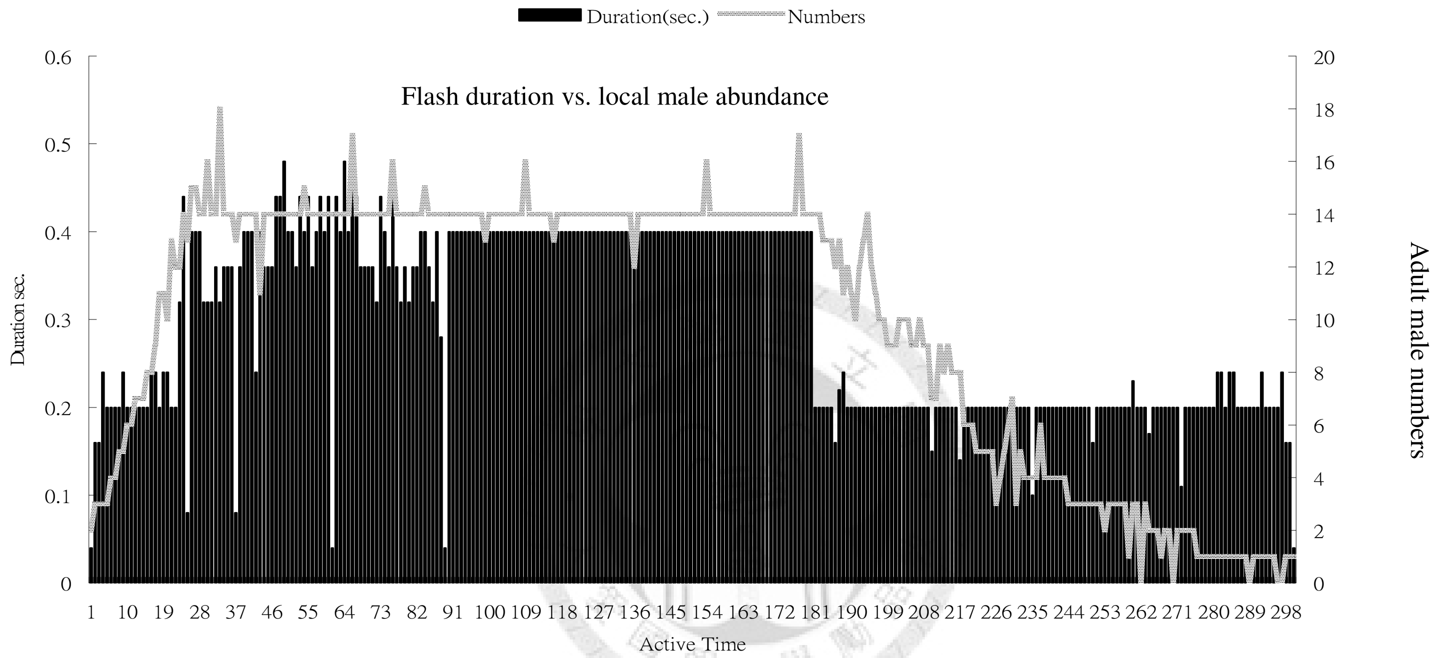

Fig. 3. The flash duration (FD) variations in male bioluminescent signals of *Luciola cerata* and their correspondence with local male abundance in a nightly five-hour activity. Averaged FD per minute changed slightly in the first 22 minutes of activity (warm-up stage), then jumped to a plateau which lasted 158 minutes (active stage), then retuned to warm-up level and remained constant until males ceased flashing (resting stage). Local male abundance was indexed by the number of males appearing in a sampling square (5x6 meters) in the first 15 seconds per minute during the nightly activity. The correspondence between FD and male abundance throughout a night was positive but weak.

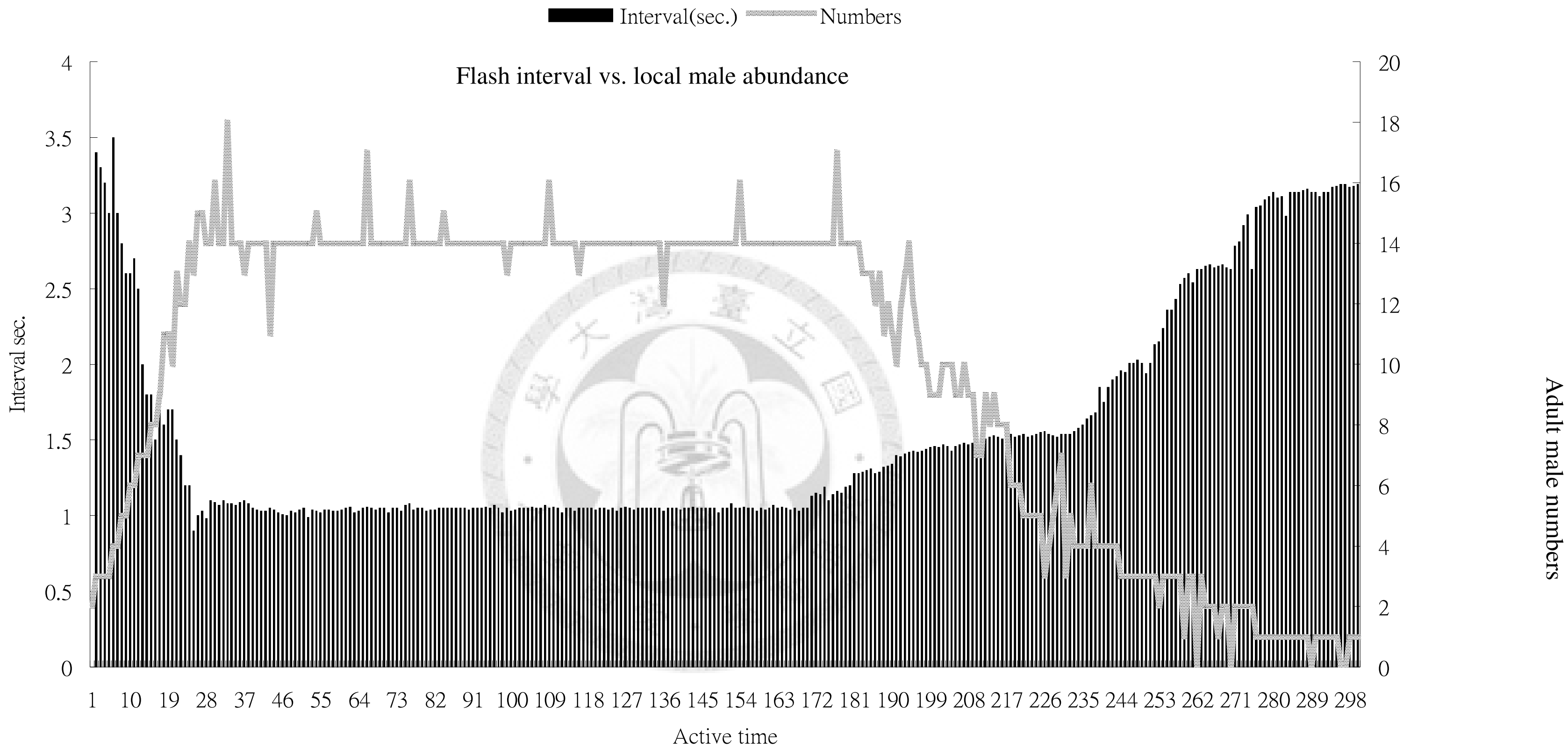

Fig. 4. The interflash interval (IFI) variations in male bioluminescent signals of *Luciola cerata* and their correspondence with local male abundance in a nightly five-hour activity. IFI exhibited a negative correspondence with the male abundance throughout the night.

Chapter 4

New trend of ecological industry- as Example of value and development of firefly watching activities in Mt. Ali area

Abstract

From June, 2003 to Dec, 2006, 2 families, 11 genera, and 42 fireflies' species were recorded in the firefly survey in the Mt. Ali area. These results show that the following adult fireflies are available for firefly watching depending on the season: *Luciola cerata* and *L. anceyi* in spring, *L. praeusta* and *L. trilucida* in summer, *Pyocoelia praetexta* and *Diaphanes citrinus* in autumn and *D. nubilus* and *D. lampyroides* in winter. Firefly specialists help visitors and the members of the local community to observe and identify the fireflies and explain why the local community should protect the firefly habitat and how to recognize the ecology of fireflies. Using the concept of biodiversity, firefly watching was created and prompted by the government as a new item for ecotourism. Gradually firefly watching in the Mt. Ali area has become a well known activity in Taiwan. The income of the Bed and Breakfast (B&B) and firefly watching tour operators in the Mt. Ali area was collected by questionnaire for the 9 month period from Jun, 2007 to Feb, 2008. The data from 31 operators were collected (not including the Mt. Ali national forest recreation area). The average operators had providing B&B and operating firefly watching tours for 7.5 years. Tours were mainly conducted mainly during the spring and summer months. Firefly watching tours were conducted between

6-9:00 p.m., lasted about 1 hour, and the B&B guests were given one free tour per evening. The total travel business income in the Mt. Ali area amounted to NTD 931,000,000 annually (not including the sale of any agricultural products). The annual income of the B&B operators during the firefly watching season (from Apr. to Jun.) and the rest of the year were NTD 52,654,560 dollars (28.67%) and NTD 131,011,920 dollars (71.33%), respectively. The monthly incomes during the firefly watching period and the non-firefly watching months were NTD 17,551,520 and NTD 14,556,880 respectively, which was a significant difference. The results show that firefly watching in the Mt. Ali area is beneficial to the B&B operator. In order to further increase the income of the B&B operators it is suggested to improve the management of the firefly watching industry and to promote the Mt. Ali area as a world class scenic area.
Key words: firefly, ecotourism, ecological industry, firefly watching, Mt. Ali

Introduction

Firefly is an important indicator species for our environment; People would realize the important of them by knowing the relationship between firefly and its ecosystem. People would also maintain and protected the biodiversity for sustain use. (Ho and Su, 2000). In Japan, Thailand, and Malaysia, their government promoted the firefly environment education and eco-guesthouse actively (Ho and Yang, 2007). This situation made the local members known how to use these special ecological resources, and the tourists also know the important of firefly conservation when they realized the beauty of nature.

The firefly biological studies are much more in past 10 years. Because of the firefly-watching activities were more and more popular, the basic taxonomy studies of Lampyridae were rich, and the phylogenetic relationship of Lampyridae of Taiwan sets up the categorized system year by year (Lai *et al.*,1998; Jeng and Yang, 2003). In addition, counties government (Ho, 1998; Ho *et al.*, 1998a, 2001,2006; Chen, 2003), national park (Yang, 1996; Jeng *etal.*, 1999a; Chang, *et al.*, 2000), travelling area (Ho, 2004), national scenic spot (Ho, 2007) and recreation farm (Wu and Yang, 2008), all had their firefly's resource investigation. These surveying results could establish the basic data and could develop plans of useless of firefly resources.

Because of successful artificial rearing technique (Chang, 1994; Chen and Chen, 1997;Ho and Chiang, 2002; Ho *et al*., 2006), fireflies could be conserved in the laboratory and there are some successful examples about firefly habitat restored, it can offer some reference for the community member in community based conservation of firefly, The other fireflies biology studies, such as flashing behavior (Ohba and Yang, 2002), life cycle (Chen *et al*., 1998; Ho, 1998; Ho and Chiang, 2002; Ho and Huang, 2003; Ho *et al*., 2002a; Ho *et al*., 2003), and management of firefly habitat (Yeh, 1999; Wu and Perng, 2007), also have results. Owing to successful case of firefly habitat recreating (Ho and Chiang, 2002) and Popular science, eco-guiding books of fireflies are published in these years (Ho and Chiang, 1997; Ho and Jong,1997; Yang, 1998; Ho *et al*., 2002b; Chen,2003; Ho, 2007). This pheromone make the general people realized the crisis and luminescence behavioral characteristic of firefly, and also awaken general people know that the numbers of fireflies are declined. In order to conserve the fireflies' population and their habitat, the popularization of the environmental education and fireflies' biology studies are more and more important.

The insect industry of Taiwan begins at Japan-occupied period. The main business items are the export tread of insect specimens and manufacture of butterflies. After the raise of the concept of biological conservation, the export tread is replaced by ecological guiding, eco tour, insect pet rising and natural enemy (Yang and Ho, 2003).

Firefly-watching activity also become an economic industry due to the activity are more and more popular year by year. In order to promote the intension of the ecological industry of firefly of Taiwan, Ho and Yang (2007) and Yang (2007) have described the ecological industry of firefly of Japan and firefly conservation. They have also introduced Japanese firefly's conservation group and firefly's museum and have some comment about firefly's ecological industry. The insect ecological industry has more new business items in recent years, government also promoted year 2001 as ecology tourist year. The eco-tour was one kind of ecological industry; it concerned local community members, environmental protection, suitable use, green, and ecology. The developments of fireflies-watching activities combine the eco-tour, and represent the new style of eco-tour.

The resources of firefly of Mt. Ali area are abundant (Ho,2006, 2007), and development of firefly-watching activity had its history, this study hopes that we can be planned and implemented with the ecological industry of firefly of Mt. Ali.. However, the development of the ecological industry of firefly of Taiwan and the output value did not have any data that is described them, so we investigated the guesthouse manager of Mt. Ali area by questionnaire. This study would become an example that how to study the firefly ecological industry in Taiwan. The results of this study would become the base of future management and administration for guesthouse managers.

Material and Method

The history and development of firefly-watching in Mt. Ali area

We used the qualitative research to study the history and development of firefly-watching in Mt. Ali area. We obtained the data by browsing through relative website, literature reviewing and open-ended interviews, the results of history and develop of firefly-watching were gotten by analyzing data via coding, and editing the story line.

The present situation and the output value of firefly-watching activity for guesthouse manager in Mt. Ali area

The firefly-watching activity was one business item of guesthouse management in Mt. Ali area, but the price and passenger's number are decided with the both sides of guest and guesthouse manager. This situation made the estimation of the output value is difficult. In order to study the present situation and output value of Mt. Ali area, we interview the guesthouse manager to know following data, the passenger numbers per month, the price of difference room type, eco-guiding situation, and situation of having a meal or not. The business volume of each firefly-watching guesthouse manager was calculated base on firefly-watching season (March to June) and non firefly-watching season (July to next February), each season was divided into holiday (Friday to Sunday) and non-holiday (Monday to Thursday). The business volume of selling agricultural product, wasabi, tea, sugar and bamboo sprouts, didn't be included.

From June 2007 to February 2008, we interviewed the guesthouse manager in Mt. Ali area (excluding Mt. Ali national forest recreation area) including, Fanlu township, Alishan township, Jhuci township and Meishan township. We used closed-ended questionnaire for our survey. The closed-ended questionnaire included two parts, the first one is the present management situation and tinier business volume, the second pats is the basic data about interviewee's materials. Part one amounts to 21 questions, the data of question 7 (the relevant advertising campaigns in fireflies-watching season) is the base for analyzing the output value of guesthouse manager in Mt. Ali area. The other questions were the data base for realizing the current situation of firefly-watching management. The interview results were summarized and made the described statistics by software Microsoft Excel 2003. The pair t-test was used to realize if there significant difference in holiday, non-holiday and in firefly-watching season or not.

Results and discussion

The present situation of firefly resources in Mt. Ali area

Ho (2006, 2007) surveyed the firefly resources in Chiayi mountain area and the results were 2 family 11 genus 42 species, These surveying results show that the firefly resource in Mt. Ali area is about 67% (42/63 x 100%) due to 63 firefly species in Taiwan (unpublished data). This result showed that there are abundant firefly biological resources in Mt. Ali area; in addition, there was different firefly adults appeared in each month. For above reason, we choice some fireflies that were easy observed for firefly-watching activity based on their population numbers. *Luciola anceyi* and *L. cerata* in spring, *L. praeusta* and *L. trilucida* in summer, *Pyrocoelia praetexta* and *Diaphane citrinus* in autumn, *D. nubilus* and *D. lampyroides* in winter.

We had also holded10 training course about firefly ecology and behavior. The main objects were the guesthouse manager and the community members, the main purpose of the course were to let the joining stuff to realize the basic biology information of firefly and there were 800 people had joined the training course. Beside the training course, we also helped the community members to hold the eco-gilding of firefly-watching activity.

The firefly-watching history and its evolution in Mt. Ali area

In early days, the lumbering and the tread of bamboo shoot were the main business for the people of Mt. Ali area. The exquisite agriculture replaced the traditional agriculture gradually due to the declines of traditional agriculture. As a results, the tea, Japan mustard (*Eutrema japonica* (Miq.) Koidz), Jelly fig (*Ficus pumila* L. var. *awkeotsang* (Makino) Corner), and sweet persimmon (*Diospyros kaki* L.), became the main agricultural product. Beside the agriculture, the community members developed the ecotourism owing to the rich biological resources. Some people modified the agriculture to the leisure service industry. According to the interview data, we know that “the mountain-climbing trail in Rui-li was the most popular route in Mt. Ali area. The visitors feel touched when they had seen the flashing fireflies flying in the tree or in valley. This situation not only awakens the visitors’ childhood memories but also made the community people to care about these fireflies”. For there were many fireflies around their land, the manager of guesthouse, Ruo-Lan, became a first protector of firefly, he saved the fireflies’ habitat by artificial weeding, raising the habitat’s humidity and increasing the larvae food. His actions promoted others guesthouse manager to save the fireflies’ habitat” In 1989, the first activity and eco-gilding of fireflies-watching were hold and attracted attention of all parties. After that, the Rui-Li area became the most famous fireflies-watching in Taiwan. At beginning, the guesthouses were small-scale and their serve terms were guest staying, repast, and agricultural product treading. Because there were abundant biological resource and beautiful nature scenery and the success of fireflies-watching activity, guesthouse manager changed their servicing terms gradually, the eco-guiding were became main business and fireflies-watching became one popular journey of eco-guesthouse management From year 2003, the Mt. Ali national scenic area administration, Chiayi county government and Chiayi forest district office hold a series of fireflies-watching activities “Dancing with firefly” to connect the slack season after the flower-watching season. The “Firefly eco-guesthouse” was the main subject for the member of guesthouse and promoted by newspaper, weekly magazine, or other kinds of media. The community members and guesthouse manager were also strive together to raise their revenue.

The present management situation of "Firefly eco-guesthouse"

According to our interview data, the guesthouse were managed by husband and wife, the employee numbers were 2 to 12 persons, and most of them were the relative or the neighbor of guesthouse manager. These part-time employees not only became the tour-guilder but also made the daily cleaning work. The management time of the longest was 60 years and minimum one was 3 years, the average time was 11 year. The investment of 10 guesthouse managers were less than 10 million NTD, and 8 managers' investment were 10~50 million NTD. The other 13 managers did not answer their investment. The average of investment of 18 managers was 16110000 NTD.

The numbers of hotel and guesthouse in Meishan, Jhuci and Alishan township were 62, 63 and 63 respectively and there were 6, 14 and 13 hotel or guesthouse announced that they offered the firefly-watching activity. However, in our result of open-ended interview, the guesthouse manager would hold the firefly-watching activity if the consumer wanted. As a result, the firefly-watching activity was the mainstream of different eco-gilding activities.

The average time of firefly-watching in Mt. Ali area was 7.5 years. The firefly-watching activity was holed in spring and summer. The firefly species for firefly-watching were *L. cerata* and *L. anceyi* in spring and time was 6~9 P.M. The firefly-watching tour was a 2 days and 1 night packaged tour including a firefly-watching eco-guiding. Most firefly-watching eco-guiding was free except one needed to charge. The firefly-watching sites were in nearby foot trial or in privately owned land and it had less safety concerns for consumer to watching in these foot trial. According to the result of questionnaire, there was just 1 case that the consumer had bit by snake and 2 cases that the consumer fallen down in firefly-watching activities. The activity duration were 1.5~2.0 hours. Before firefly-watching beginning, the manager had some oral introduction of firefly ecology and conservation or by broadcasting the video type of firefly ecology and advertised their firefly-watching rules. After explanation, the manager had their firefly-watching activities in their site. 14 guesthouse managers provided red glassine or LED flashlight to reduce the light pollution during firefly-watching. The other guesthouse manager didn’t provide these tools.

Although there were qualitative results of firefly species in Mt. Ali area, the quantitative results were still absent. We used the question No. 9 that listed in our questionnaire to make the guesthouse managers estimating the firefly population size. Although it was not precise way, the guesthouse managers were all local community resident. We could know the firefly population change in Mt. Ali by guesthouse managers' daily observation. According to our result, 18 guesthouse managers thought that firefly population numbers were stable, 9 managers thought it increased and 4 managers thought it decreased. According to the interview results of 9 managers that thought firefly population numbers increased, they thought this situation could owe the reduction of pesticide application. The other 4 managers thought that firefly population decreased, they thought this situation could owe to the climate changing and the increase of residential area.

The output value of firefly-watching activity in Mt. Ali area.

From June 2007 to February 2008, we interviewed 31 guesthouse managers; the gross earnings were 186,245,280 NTD for these 31 guesthouse managers. We evaluated that the gross earnings were 931,000,000 NTD excluding agricultural product in Mt. Ali area. The hotel industry was relative small scale, all members were guesthouse or small hotel managers and there had not resort or grand hotel in Mt. Ali. Most visitors were family tourist. The monthly holiday gross earnings were 24,948,480 NTD and it was significant higher than monthly non-holiday gross earnings, 7,159,920 NTD ($p = 0.002$, $\delta < 0.05$, paired t-test). The guesthouse management was a part-time activity for local guesthouse managers in holidays. In non-holidays, guesthouse managers had their farming activities in their land and selling agricultural product was main item. It was a relative plastic living style for these part-time guesthouse managers.

The monthly gross earnings in firefly-watching season and non firefly-watching season

The gross earnings of firefly-watching season (April to June) were 52,654,560 NTD, about 28.67% of annual gross earnings. The gross earnings of non firefly-watching season (July to next March) were 131,011,920 NTD, about 71.33% of annual gross earnings. The monthly gross earnings of firefly-watching season were 17,551,520 NTD (54%) and had significant difference to monthly gross earnings of non firefly-watching season, 14,556,880 NTD (46%) ($p = 0.023$, $\delta < 0.05$, paired *t*-test，Fig. 2). the holiday monthly gross earnings of firefly-watching season were 13,432,000 NTD also higher than the non holiday monthly gross earnings, 4,119,520 NTD. The holiday monthly gross earnings were 3.5 times than non holidays' ($p = 0.027$, $\delta < 0.05$, paired *t*-test，Fig. 3). Comparing the gross earnings of firefly-watching season and non firefly-watching season, it was a high ratio that the gross earnings of firefly-watching season were 28.5% of annual gross earnings. It was guesthouse manager's off season from April to June before firefly-watching activity be hold. Firefly-watching could attract more tourists to go to Mt. Ali area and increased the lodging ratio of guesthouse, sales volume of agricultural products as tea, bamboo shoot and plum.

The monthly holiday gross earnings of firefly-watching season and non firefly-watching season

According to the results, the holiday gross earnings of firefly-watching season were 13,432,000 NTD, it was significant higher than gross earnings of non firefly-watching season, 11,516,480 NTD (p = 0.002, $\delta < 0.05$, paired t-test，Fig. 3). The holiday lodging ration of firefly-watching season was 100%, and 95% in non firefly-watching season. It demonstrated that most tourists like to go to Mt. Ali's guesthouse on holiday. This situation was regular form for guesthouse manager in Mt. Ali.

The monthly non-holiday gross earnings of firefly-watching season and non firefly-watching season

According to the results, the holiday gross earnings of firefly-watching season were 4,119,520 NTD, it was significant higher than gross earnings of non firefly-watching season, 3,040,400 NTD (p = 0.028, $\delta < 0.05$, paired t-test, Fig. 3).Although the lodging ratio of non holiday in firefly-watching was not high; it was still higher than those in non firefly-watching season. The main tourists of firefly-watching activity were family guest and young people; as a result, the firefly-watching was popular in holidays. The local manager thought that the difficulty of their present management was the low tourists' numbers in non holiday. Increasing the non holiday lodging was the answer for this dilemma by promoting the non holiday selling activities, increasing the management qualities of guesthouse, attracting oversea tourists and using the online booking.

The gross earnings of firefly-watching season and summer or winter vacation

The monthly gross earnings of firefly-watching season were 17,650,320 NTD, it was significant higher than those of summer or winter vacation, 14,810,480 NTD (p =0.005, $\delta < 0.05$, paired t-test). This phenomenon demonstrated that the tourist numbers increasing was not correlated with summer or winter vacation, and owing to firefly-watching activity, the tourist number and gross earnings were increased.

The management difficulty of guesthouse manager in Mt. Ali area and their solving methods

(1). Training the eco-guiding stuff or providing eco-guiding material:

According to the interview results, the firefly eco-guilders were guesthouse manager's job. Their knowledge of fireflies' ecology were came form their daily observation and had less contents in their guiding; Beside that, owing to the financial support, there were not others eco-guider could support the firefly-watching eco-guiding. This situation made the guesthouse managers thought that it didn't have enough eco-guider in Mt. Ali area. So, the eco-guider training of firefly-watching activity needed to hold continually. In addition, we suggest that the administrator of national scenic area of Mt. Ali and Chiayi forest district office needed to induce the eco-guiding volunteers during firefly-watching season to raise the quality of firefly-watching activity;

Some visions of firefly eco-guiding disks were old and needed renew vision.

(2). Reinforcing the media promoting and printing folding producing:

Let more people realized the beauty of fireflies' bioluminescence and their brief biological data by different kinds of media. Proposing that the local government could compile the advertising budget, cooperate with the firefly-watching planning, promoting the firefly-watching activity. Besides that, the present firefly's propaganda material had too professional content. During arranging and publishing these propaganda, they should personalize and more oral content.

(3). Popularizing firefly-watching activity in autumn and winter:

There were differential fireflies' species in each season; we suggested that *Pyocoelia praetexta*, *Diaphanes citrinus*, *D. nubilus* and *D. lampyroides* in autumn and winter were also suitable species for firefly-watching activity. The bioluminescence of these fireflies was difference with *Luciola* firefly in spring; the firefly fauna had the surveying results (Ho, 2007), the guesthouse manager also known that firefly-watching activity could be hold in autumn and winter. The suitable place for autumn and winter firefly-watching activity was in mountain area that above sea level 2000 meter. For the safety reason, autumn and winter firefly-watching activity was not popularized. This question needed government and guesthouse manager to solve together.

(4). Participating in the marketing of international eco-tour:

Selecting the ecological community with the good image at the national scenic area of Mt. Ali, evaluated their firefly habitat restoring, package tour, ideal production of firefly and environmental maintenance in the community by expert, all the community that reached the standard, was recommended and assisted to participate in the international tourism exhibition in Asian-Pacific area by the administrator of national scenic of Mt. Ali. It would not only promoted the beauty of Taiwan's firefly but also made the opportunity for the firefly ecological recreation manager having chance to exchange with foreign personages, to promote the eco-tour quality of local community.

The firefly sustainable management in national Mt. Ali scenic area

The development of eco-tour of the national scenic area of Mt. Ali was different from general pleasure travel. There are the goals of the economy, society and environment in the eco-tour, and the priority of these goals, need constant discussion and adjustment, via the efforts of the guesthouse manager and government. In the community participates in, the development of nature reserve demonstrated that only when the local community supported the natural environment in all world, the work of the natural conservation could be pursued smoothly. There was a close relationship between the local community could obtain the financial benefits and their attitude toward species or environment conservation. On the premise of combining community's economic development and natural conservation, improving the community members' income, and members who get benefit would join in natural conservation work, and the relative work of firefly conservation could supported by local resident. Community people resorted the firefly habitat and provided a environment for firefly-watching. These situations would attract tourist to watch fireflies and would create the benefits for community residents, then the sustained use of firefly resource in Mt. Ali was possible.

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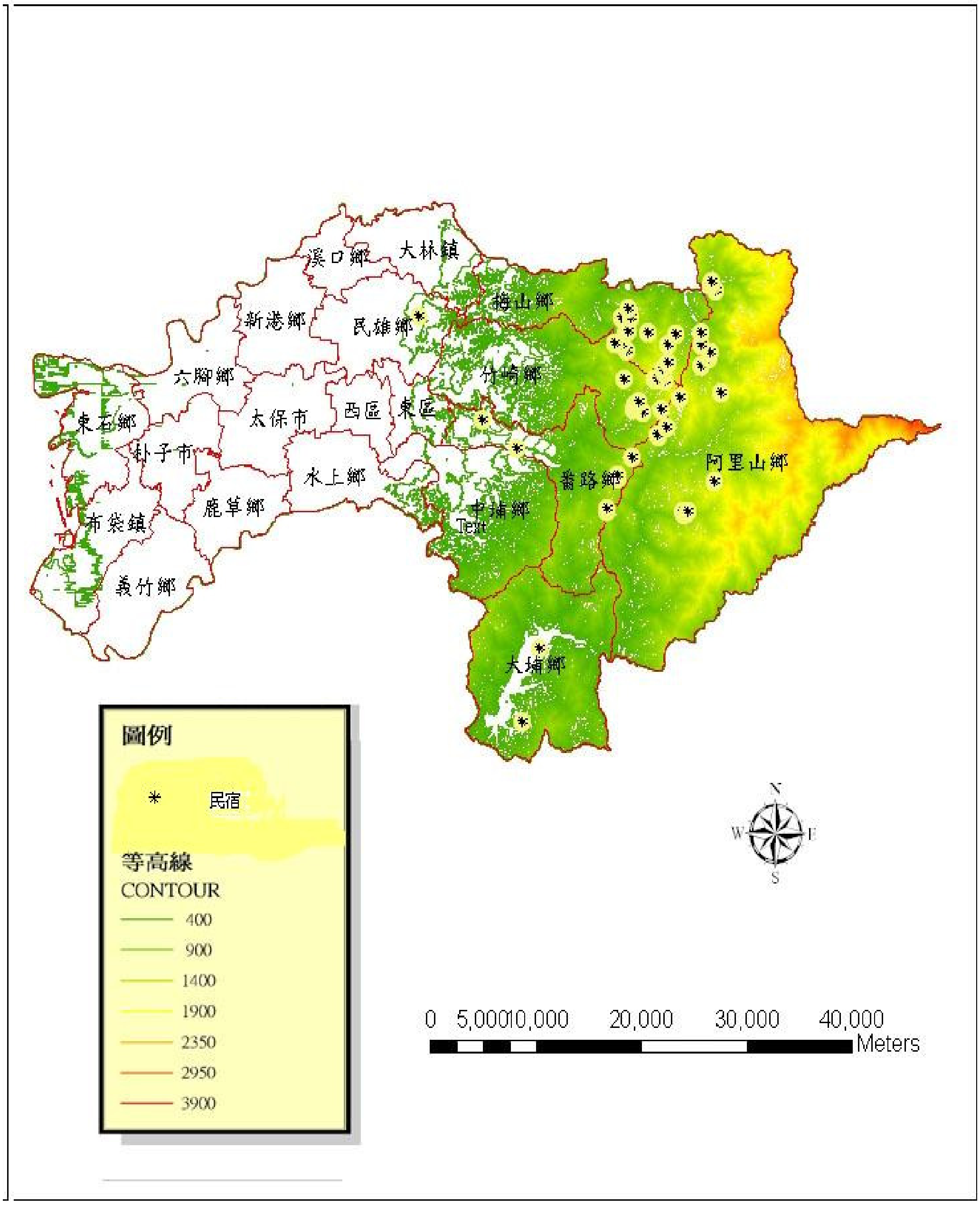

Fig. 1. The map of 31 visited boarding house in Mt. Ali.

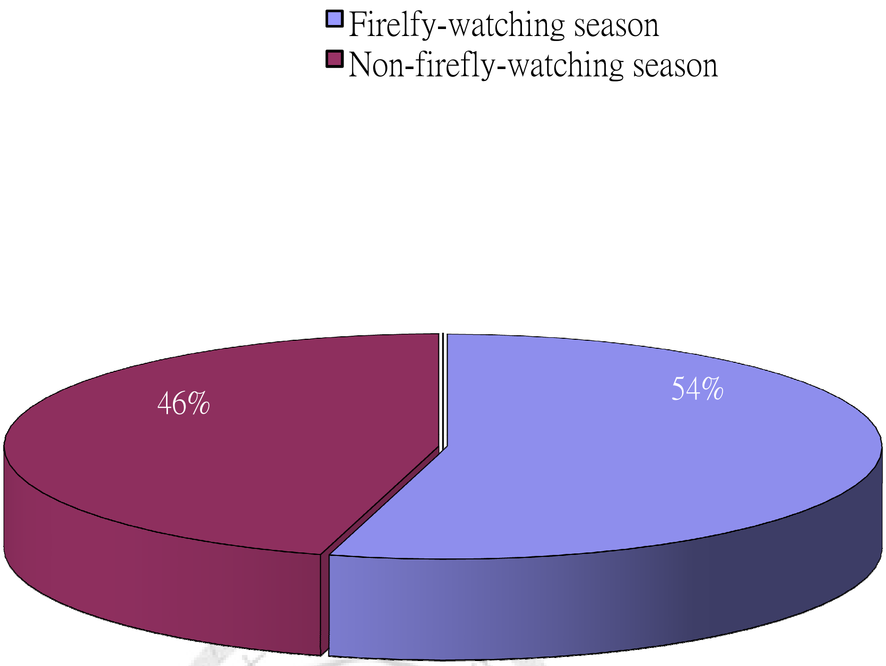

Fig. 2. Comparison of output value of ecological industry at Mt. Ali area in firefly watchig season and non-firefly watching season (P value= 0.023, $\delta < 0.05$， paired t-test).

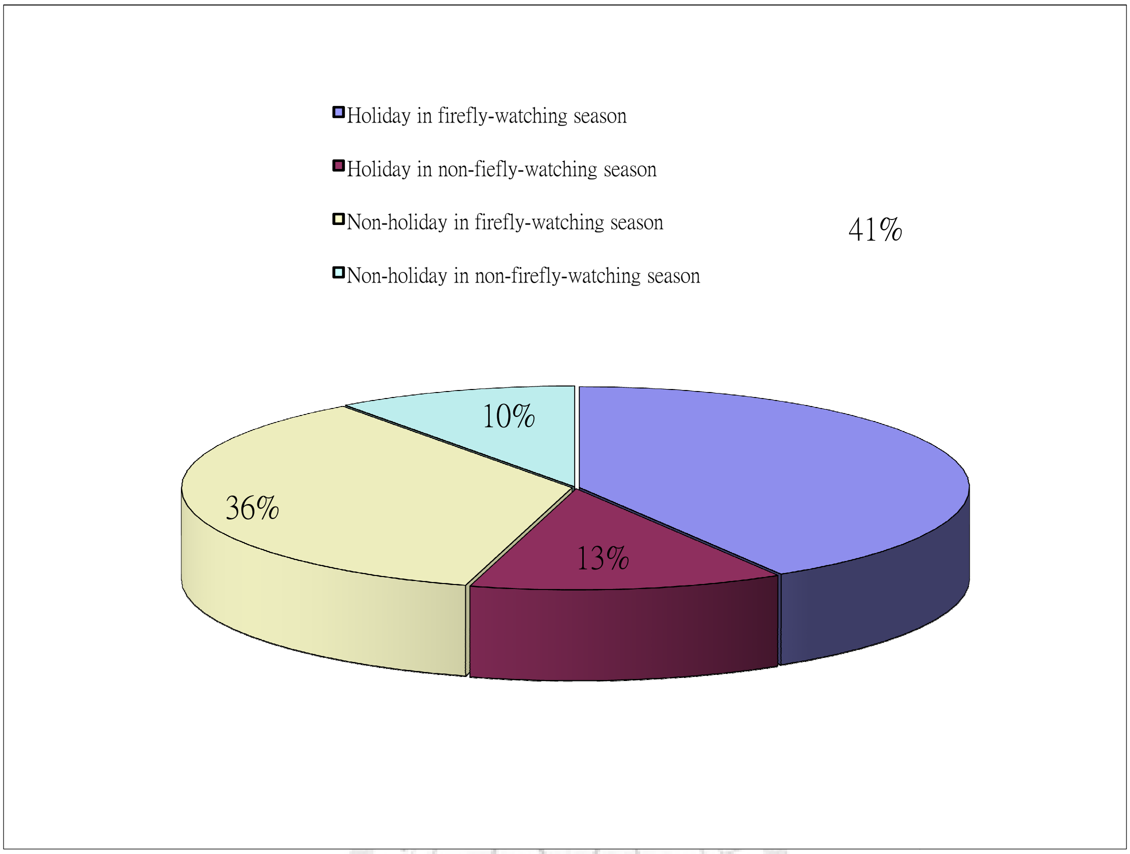

Fig. 3. The comparison of output value of ecological industry at Mt. Ali area (holiday and non-holiday in firefly watching and non firefly watching season).

表一、阿里山螢火蟲生態產業之市場價值評估問卷

Table 1. The Questionnaire of firefly ecological industry at Mt. Ali area

第一部份—經營現狀

1.請問您已開業幾年？ 從　　　至　　　，共　　　　年。

2.營業至今所投資額約：

□小於 1000 萬□1000 萬～5000 萬 □5001 萬～1 億 □大於 1 億

□　　　　萬元

3.員工人數：

自家人：　　　　人　　　　　　　　　　　　外聘員工：專職：　　人、兼職　　人

4.賞螢歷史沿革：□有辦理賞螢活動，至今已有　　年

□沒有辦理賞螢活動

5. 每年的「螢火蟲季」時間

春季是：　月～　月，種類有　、　、　、　、

夏季是：　月～　月，種類有　、　、　、　、

秋季是：　月～　月，種類有　、　、　、　、

冬季是：　月～　月，種類有　、　、　、　、

6. 每年的「螢火蟲季」地點

春季是：

夏季是：

秋季是：

冬季是：

7.請問您是否在每年的「螢火蟲季」推出相關的促銷活動(如住房優惠、螢火蟲專案)？促銷活動時間是：　月～　月，活動名稱

螢火蟲季						非螢火蟲季					
假日			非假日			假日			非假日		
人數	條件	價錢	人數	條件	價錢	人數	條件	價錢	人數	條件	價錢

8. 「螢火蟲季」是否提供螢火蟲導覽服務，□有，□沒有

一天幾個場次　　　次

一場導覽要多久時間　　　小時

導覽服務是否收費？

□住宿遊客沒有另外收費，□沒住宿遊客有收費，收費標準　　　　元

導覽服務自行帶隊 □是，□否

一場次須要　　位解說員

解說員一次費用　　　　元

9. 依據您的觀察，當地螢火蟲數量是逐漸減少、增加或維持不變？

(1) □減少　　主要原因

(2) □增加　　主要原因

(3) □維持不變

10. 螢火蟲季時是否曾經發生安全問題？如何解決？（可複選）

□跌倒 □蛇咬 □蜂螫 □其他意外

發生安全問題如何解決

11. 是否為遊客提供賞螢觀賞工具（可複選）

□手電筒 □放大鏡 □紅色玻璃紙 □其他工具

12. 為遊客進行螢火蟲導覽服務之前，是否有提供其他服務？（可複選）

□導覽之前解說 □摺頁 □其他資料

13. 請問您主要是提供那些服務？（可複選）

□住宿 □餐飲 □農特產品銷售 □生態導覽解說 □文化創意產品 □其他

14. 除螢火蟲季之外，非螢火蟲季有無其他導覽服務？

□動物生態　如：　　　　　　　時間

□植物生態　如：　　　　　　　時間

□文化　　　如：　　　　　　　時間

□其他　　　如：　　　　　　　時間

15. 文化創意產品主要為何種？

□ 衣服 □ 杯子 □ 扇子 □手提燈 □手機吊飾 □ 玩偶 □手工藝品 □ 其他

16. 目前貴單位有無接受政府協助、輔導？

中央政府 □有，□沒有

地方政府 □有，□沒有

17.貴場所對於螢火蟲季活動或螢火蟲棲地有何投資？

□棲地鋤草　金額　　　　元

□活動宣傳　金額　　　　元

□印刷螢火蟲相關資料　金額　　　　元

18. 目前在經營上面對哪些困難？

19. 如需政府輔導，需要哪方面的協助？

□報章雜誌、平面媒體

□電子媒體宣傳、網路

□安排螢火蟲解說人員教育課程

□提供摺頁相關教材支援螢火蟲導覽

20. 螢火蟲季貴場所舉辦的各種活動對於貴場所的利潤是否有提升效果？

□有

□沒有原因

21. 您認為螢火蟲資源之永續利用及螢火蟲季的舉辦對於貴場所之經營是否有正面之幫助？

□有

□沒有　原因

第二部分—受訪者資料

店名：

主要營業項目：

聯絡人及聯絡方式：姓名　　　　　　　　電話：　　　　　　　傳真：

e-mail:

Chapter 5

The conservation strategies of *Luciola cerata* Olivier

The black-winged firefly, *Luciola cerata* Olivier, 1911 is a widespread firefly species below altitute 1500 meters. It is also the most abundant firefly and the main species for firefly-watching activities from March to May in Taiwan. According to Zhao *et al*. (2009) estimating criterion, the black-winged firefly is 48 points and could be listed in third protected degree, though the black-winged firefly is not in name list on the protected insects now.

Flagship, keystone, umbrella and indicator species have various meaning and purpose in conservation biology and use in conservation strategy. Some flagship species are larger mammals and birds (ESCAP, 2007), and some are the bird-wing butterflies or larger beetles (IUCN, 2010). One character of flagship species is for bringing the concern of the public people. The image of these species also becomes the logo for some international conservation society, for example, the panda for WWF (World Wildlife Fund). The black-winged firefly has the potential to become the flagship species of the fireflies conservation in Taiwan owing to the firefly-watching season from March to May and it’s the main species for firefly-watching. Furthermore, the habitat of *L. cerata* is also the habitat for the other *Luciola*, *Aquatica* , *Curtos*, and *Pyrocoelia* fireflies that have relative less population number than the population number of *L. cerata*.

The firefly-watching activities were more and more popular from 1996. At beginning, some unlimited or poor-planning firefly-watching activities made a large damage for *L. ceata* population beside the habitat loss and light pollution. The firefly-watching activity in Nei-wan community, Hsin-chu county ever suspend form year 2005 to 2007. One character of a poor firefly-watching activity is that there were not enough narrators and some tourists with less ecological concern caught *L. cerata* individual during watching firefly. This pheromone makes the *L. cerata* numbers decreased quickly during firefly-watching season. However, owing to *L. cerata* is a non-protected wild animal, and the huge out value of firefly ecotourism in Taiwan (Ho *et al*., 2009). A limited firefly-watching activity, well-planning firefly-watching season project and the continuing firefly ecological education are relative suitable methods for the conservation of *L. cerata*. Although there were some poor-planning firefly-watching activities at beginning, after the firefly ecology education was wide-separated by many local conservation societies, most tourist know the basic rules during firefly-watching now.

The concern of community-based conservation was another important mater in a well-planning firefly-watching project. During the surveying period, the author known that the community with abundant firefly resource, their members always organized their patrol party to avoid some tourist caught firefly. A well-planning firefly-watching project should let the community members to get the benefits from firefly-watching activity not only businessman (www.peopo.org/portal.php?op=viewPost&articleId=16251).

The basic of firefly ecological education was the firefly's biology. The results of this study could become the teaching and interpreting materials of ecological education for public after suitable converting. The author used the studying results of his master thesis and this study serve as a firefly-watching narrator from 1998.

Although marking-release-recapture (MMR) or transect sampling method were used for monitoring *L. cerata* and *Pyrocoelia praeusta* population numbers in central Taiwan (Wu and Yang, 2008). The monitor of *L. cerata* population numbers is still a problem for local community members and the indigenous people in Taiwan owing to the abundant firefly resource, less classification ability and population numbers surveying skill for fireflies.

Ho *et al*. (2009) ever used the questionnaire to make the guesthouse managers estimating the firefly population size in Mt. Ali area, but it's still not a precise and authentic way.

One possible solving method is using the digital camera to shot the bioluminescence of *L. cerata* and use some software to analyze the light spot in the picture, but it needs to test its accuracy. (Ho, personal communication).

According to the unpublished data of the flash patterns in south Taiwan and mitochondrial DNA, the black-winged firefly in San-min (Namasia township, Kaohsiung county) had relative longer flash interval than the black-winged firefly in center and north Taiwan. The phylogenetic tree of mtDNA (CO II) also revealed two major clades: HS (San-min population) and the other populations. This phenomenon was similar to the results of the Japanese aquatic firefly, *Luciola cruciata* in east and west Japan. The flash interval of east Japan *L. cruciata* were longer than the flash interval in west Japan *L. cruciata* (Tamura *et al*., 2005). The phylogenetic tree showed that there were three clades (Kyushu, west Japan and east Japan) in different *L. cruciata* populations. Based on these molecular and ecological data, the author suggests that the black-winged firefly in Namasia township should have a protected area to keep its population. Reconstructing engineering of Namasia township after flood in August 8, 2009 should concern to save the habitat of *L. cerrata*. It's not owing to the science reason but also the culture of indigenous people. The firefly habitat of *L. cerata* in Namsia township was also the traditional area of Bunun tribe.

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Evidence for Two Male Morphs of *Luciola cerata* Olivier (Coleoptera: Lampyridae) Exhibiting Distinct Mating Behavior, with Implications for Sexual Selection

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Abstract

The black-winged firefly, *Luciola cerata* Olivier, is endemic to Taiwan and is the most common firefly on the island. Males flash spontaneously and females respond with bioluminescent flashes at fixed response delays. In order to explore the potential for sexual selection in *L. cerata*, we surveyed males at 12 sites in Taiwan. We measured variation in male morphological characteristics and mated males to females. Male flash behavior and mating success was quantified under a variety of experimental sex ratios in the lab. We found there are two male morphs of this species, which are distinguishable only by the morphology of the lantern. One morph has a pentagonal second light segment, while the other has a semi-oval second light segment and only produces a flash with the first lantern segment. Besides this difference in morphology, the flash patterns and mating behavior also differ between these two morphs. Males with a pentagonal segment have a faster flashing rate than those with a semi-oval segment and are considered more attractive to females in groups with male-biased sex ratios. Furthermore, females that mate with the pentagonal-segment morph demonstrate greater fecundity than those that mate with the semi-oval-segment morph.

Key Words: firefly, flashing rate, male dimorphism, male competition, mating behavior

Males in many animal species show variation in morphology which is associated with differences in behavior (Austad 1984; Dominey 1984; Travis 1994). For example, large and small males frequently utilize strikingly different behaviors to encounter and mate with females (Dominey 1980; Rubenstein 1980, 1987; Howard 1984; Gross 1985; Kodric-Brown 1986; Arak 1988; Reynolds *et al.* 1993). Occasionally, variation on male morphology is dimorphic and two or more distinct male forms co-occur in populations with intermediate forms scarce or lacking (Shuster 1987; Ryan and Causey 1989; Zimmerer and Kallman 1989; Danforth 1991).

The horns of some male beetles were the classic example of morphological dimorphism (Darwin 1871; Wallace 1878; Inukai 1924; Huxley 1931; Beebe 1944; Arrow 1951; Clark 1977; Cook 1987; Siva-Jothy 1987). In these species, male horns have been shown to function in intra-sexual combat over access to females (Palmer 1978; Eberhard 1979,

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1987; Brown and Bartalon 1986; Goldsmith 1987; Siva-Jothy 1987; Conner 1988).

Mating behavior and the mechanisms of sexual selection vary greatly across the many known species of fireflies. It has been predicted that much of this variation depends upon the status of nuptial gift production in each species, as females are apparently polyandrous when nuptial gifts provide material benefits (see Lewis and Cratsley 2008 for review). Such nuptial gifts have the ability to potentially increase a female's lifetime fecundity, thereby resulting in selection for both polyandry and post-copulatory female choice (Boggs 1995; Vahed 1998; Gwynne 2008). Lewis and Wang (1991) found that *Photinus aquilonius* Lloyd and *Photinus marginellus* LeConte are polygamous and mating behavior appears to be affected by predictable seasonal shifts in operational sex ratios, such that male-male competition and female choice prevail early in the flight season, while interfemale competition and male selectivity may predominate later in the season. *Photinus collustrans* LeConte is another example. Males are largely monogamous, lacking the ability to produce nuptial gifts, and they seek brachypterous females at twilight. Females remain mostly motionless, signaling to males flying above. Once mating is complete, the females return to their underground burrows (Wing 1984, 1988, 1989, 1991). Branham and Greenfield (1996) demonstrated that female *Photinus consimilis* Green prefer flash rates that exceed the mean rate in the male population and flash lengths that approximate the mean. *Photinus pyralis* (L.) is another example of how sex ratios affect mating behavior and sexual selection. In populations with a low male density, females prefer large males, but as male-male competition increases, small males have an opportunity to mate because they move faster than large males (Vencl and Carlson 1998).

Courtship behaviors by many fireflies in the genus *Luciola* Laporte consist of short bioluminescent flashes, but are considerably complex and highly varied (Papi 1969; Lloyd 1972, 1973, 1974; Ohba 2004a, b). For example, in the case of *Luciola cruciata* Motschulsky, males flash synchronously while in flight (Ohba 1984, 2004b). Females flash spontaneously as well as in response to male signals. Flying males are attracted to flashing females, land nearby, and display diverse flashing behaviors before contact and copulation occur.

Luciola cerata Olivier, the black-winged firefly, is a species endemic to Taiwan (Lai *et al.* 1998), with a wide distribution from sea level to an elevation of 1,500 m (Jeng *et al.* 1999). Like many firefly species, this species has a sexually dimorphic lantern. The lantern in males has two segments capable of producing the characteristic bioluminescent flash. Males also have relatively large compound eyes and a relatively small body size. Females, on the other hand, have a single-segment lantern, smaller compound eyes, and a relatively large body size. Adults emerge in March and remain until May. During this period, they can be found in various habitats, including densely vegetated sloping fields, forest trails, and unlit roads. Many of their habitats are characterized by high humidity, and they are especially abundant in areas lacking light pollution.

Reports of the bioluminescent signaling behaviors of Taiwan's *Luciola* fireflies are quite scarce, and these behaviors remain understudied. Ohba and Yang (2003) reported on the bioluminescent behavior and communication system of *L. cerata* in the field. The communication system is classified to be of the HP variety, which means that the female responds to the male at fixed intervals. Ohba and Yang (2003) were the first to document *L. cerata*'s mating biology, but the details of the mating system are still unknown. In our study, we observe the courtship interactions between males and females of this firefly as a function of different sex ratios. Female behavior and subsequent fecundity in different groups were also recorded. We also demonstrate the existence of two distinct male morphs that exhibit two types of mating strategies, a phenomenon that has not been documented in any other lampyrid species to date.

Material and Methods

Morphological Characteristics of Male *Luciola cerata*. Seventy-seven fresh males of *L. cerata* were frozen at -20° C for 30 min. The shape and size (length and width) of the second lantern segment and the body length, width, and weight of each male were determined with a stereomicroscope (Leica MZ16) and electric balance (AND ER-120A). Body length and width, head width, pronotal width, elytral length, and lengths and widths of first and second lantern segments were measured for another 29 dried males.

Field Census of *Luciola cerata* Males. During the spring of 2006, 12 survey sites were visited (Fig. 1) and adults of *L. cerata* were collected from all 12 sites. These survey sites were all sloping fields densely vegetated with shade-loving plants. Three sites (Wu-Lai, Rui-Sui, and Tung-Shih) were along forest trails; the other nine sites were on unlit roads. We used sweep nets to capture male *L. cerata* from a 5 m × 5 m area from 7:00 to 7:10 PM. Other species could be distinguished by their flickering flashing patterns (*e.g.*, *Luciola filiformis* Olivier) or light coloration (*e.g.*, *Luciola kagiana* Matsumura), and these fireflies were not caught during the census.

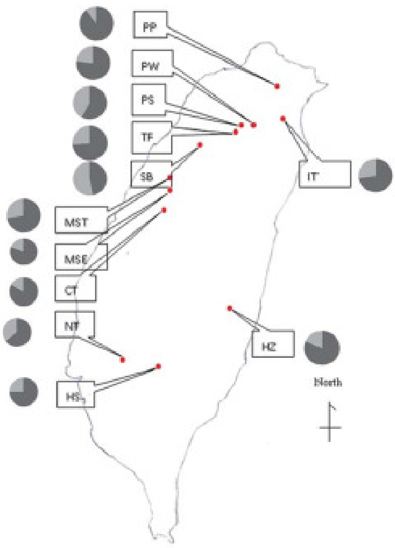

Fig. 1. Locations of survey sites for *Luciola cerata* in Taiwan. HZ: Hualien Rui-Sui (23°35′18.8″N 121°21′15.5″E, Hualien county, 3/30/2006); IT: Ilan Tou-Cheng (24°50′56″N 12°47′13″E, Ilan county, 4/19/2006); PP: Taipei Pin-Shih (25°1′31.9″N 121°44′2.4″E, Taipei county, 4/20/2006); PS: Taipei San-Xia (24°50′09″N 121°27′08″E, Taipei county, 4/21/2006); PW: Taipei Wu-Lai (24°49′31.3″N 121°31′28.8″E, Taipei county, 4/12/2006); TF: Taoyuan Fu-Xing (24°42′58″N 121°21′41″E, Taoyuan county, 4/18/2006); SB: Sinzhu Bei-Pu (24°40′21″N 121°03′53″E, Shizhu county, 4/6/2006); MST: Maioli Shi-Tan (24°31′22″N 120°55′10″E, Maioli county, 4/17/2006); MSE: Maioli San-Yi (24°23′36″N 120°45′55″E, Maioli county, 4/16/2006); CT: Taichung Tung-Shih (24°16′35.8″N 120°50′41.7′E, Taichung county, 4/15/2006); NT: Tainan Tung-San (23°16′51″N 120°25′54″E, Tainan county, 4/15/2006); HS: Kaohsiung San-Min (23°15′38.7′N 120°42′6.9″E, 3/21/2006).; The circular chart for each site represents the ratio of pentagonal males (dark gray) and semi-oval males (light gray).

Fecundity. Sixteen pairs (13 males with pentagonal second lantern segments [henceforth referred to simply as pentagonal males] and three males with semi-oval second lantern segments [henceforth referred to as semi-oval males] with 16 females) of laboratory-reared adult *L. cerata* were used. We paired one laboratory-reared male and one laboratory-reared female in a round, transparent plastic box (8 cm high × 10 cm wide) for mating. The same was done for another 10 pairs (two pentagonal and eight semi-oval males with 10 females) of field-captured individuals. After copulation, each mated female was placed singly in another round, transparent plastic box with a 40×40×2 mm sponge for egg-laying until she died. Number of eggs on the sponge was determined by visual counting with a Leica MZ16 stereomicroscope.

Mating Behavior. Virgin laboratory-reared males and females were individually placed in a round, transparent plastic box (8 cm high × 10 cm wide), and their flashing behavior was recorded using a Sony TRV-30 camera. These observations of individuals visually isolated from any other fireflies served as a control for subsequent experiments with altered sex ratios. To identify the different individuals, we used a color pen (SC-S-M, SUPER COLOR, PILOT, Japan) to mark the elytra with small, differently colored dots.

In 2008, the interaction between males and females in groups were recorded by camera. Groups with a male-biased sex ratio were: two males (one pentagonal, one semi-oval) + no females; two males (one pentagonal, one semi-oval) + one female; four males (two pentagonal, two semi-oval) + one female; 12 males (seven pentagonal, five semi-oval) + one female; and eight males (five pentagonal, three semi-oval) + three females. Groups with a female-biased sex ratio were one pentagonal male + two females and two males (one pentagonal, one semi-oval) + three females. Another two groups with female-biased sex ratios, two males (one pentagonal, one semi-oval) + three females and five pentagonal males + six females, were utilized in experiments conducted in 2009. Flash duration and flash interval in all control and experimental groups were measured in a frame-by-frame analysis using Windows Movie Maker.

Statistical Analysis. SYSTAT statistical software version 10.2 (Systat Software Inc.) was used to perform all statistical analyses. In the experiments testing for differences between male fireflies, one-way analysis of variance (ANOVA) was used with $\alpha = 0.05$. Means are reported with their standard error of the mean.

Results

Morphological Characteristics of Male *Luciola cerata*. Males of *L. cerata* exhibit dimorphism in the shape of the second lantern segment (Fig. 2). Fresh specimens of pentagonal males have relatively greater body length and width, weight, and second lantern segment size than semi-oval males (Table 1). The results are similar for dried specimens of male *L. cerata*, but in addition to differences in the four aforementioned variables, pentagonal males also have relatively greater protonal width and elytral length than semi-oval males, although the differences in the head width and size of the experimental groups, males crawled and engaged in flash dialogues with the females. In groups with two males of different morphs (1 pentagonal and 1 semi-oval), the pentagonal male crawled around the box, and its flash interval changed from 1.10 ± 0.25 sec (mean ± SE) to 9.92 ± 0.58 sec (Fig. 3). While the pentagonal male was flashing and crawling, the semi-oval male merely remained motionless on the wall and did not flash. After 10 min, the pentagonal male stopped flashing and also remained stationary on the wall.

Flash duration was about 0.16–0.19 sec for both male morphs in male-biased and female-biased groups. Flash interval of semi-oval males was 4.19–5.14 sec, whereas it was shorter for pentagonal males (3.31–4.06 sec) in the groups with a male-biased sex ratio (Table 2). When the sex ratio was female-biased, the flash interval of pentagonal males was shorter than that of semi-oval males (Table 3).

In groups with a male-biased sex ratio, most females preferred mating with pentagonal males (n = 5), whereas only one female mated with a semi-oval male. In groups with a female-biased sex ratio, five females mated with pentagonal males, but only two females mated with semi-oval males. In the male-biased groups, the response delay time of the female mating with a semi-oval male was longer than that of females mating with pentagonal males (Table 2). When mating with semi-oval males, female response delay time was quicker in the female-biased groups than in the male-biased groups.

Females found a mate and began copulating quicker in the male-biased groups than in the female-biased groups. Time of initiation of first copulation was much shorter for pentagonal males than for semi-oval males regardless of sex ratio bias

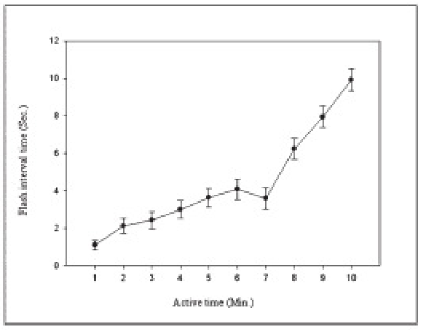

Fig. 3. Average flash interval of pentagonal male *Luciola cerata* (n = 178) over time, when grouped with one semi-oval male.

(Tables 2 and 3). First mating duration was also much longer by pentagonal males than by semi-oval males (Tables 2 and 3). In the male-biased groups, males mated only once. In the female-biased groups, two pentagonal males mated twice, and the mating duration each time was 160–166 min (Table 3).

While a female and her chosen mate were engaged in dialogue, other males attempted to mate with her. These males would crawl to the female, mount her dorsally, and directly extend their genitalia without attempting any kind of flash communication with her. Invariably, the female would not accept these attempts at copulation and would instead only accept the attempts of the communicating male. Once copulation had begun, other males would still attempt to mount the female, but these attempts were unsuccessful. However, after copulation was completed, the unmated males did not attempt a second copulation with the female that had just mated. This might be attributed to the presence of the male's spermatophore in the female's reproductive tract.

Discussion

There is a distinct size difference between the two male morphs of *L. cerata*. Males with a pentagonal second lantern segment are larger than males with a semi-oval second lantern segment. This size difference affects the mating behavior and mechanisms of sexual selection in *L. cerata*. Similar to *P. pyralis*, large males have a better opportunity to mate, but small males still have a chance as mating competition increases (*i.e.*, when the male/female sex ratio is high) (Vencl and Carlson 1998). However, there are some differences in the male-male competition modes in these two firefly species. The male-male competition among large individuals of *L. cerata* and *P. pyralis* is based on the ability to attract females through flashing behavior. On the other hand, the type of competition among small individuals of *P. pyralis* is scramble competition (via mobility), whereas small individuals of *L. cerata* use an alternative tactic, because semi-oval males flash have one light segment. Adult *L. cerata* of both sexes live up to two weeks and drink only water (Wu and Yang 2008). Adults emerge in March and remain until May (Jeng *et al.* 1999; Wu and Yang 2008). The courtship of pentagonal males using two light segments to flash may cost more energy than the courtship of semi-oval males flashing with only one light segment. This phenomenon may diminish the life span of pentagonal males compared to semi-oval males, regardless of climate, predators, or other mortality factors that affect the male life span. During March and April, females prefer mating with pentagonal males. However, in the latter part of the mating season, females have relatively less choice to mate with a pentagonal male owing to the decreasing proportion of pentagonal males. During the late mating season, female *L. cerata* may mate more often with semi-oval males due to their greater numbers in proportion to pentagonal males.

Female *L. cerata* are monogamous and they prefer to mate with a pentagonal male, which may have a relatively larger spermatophore. This may explain why females that mate with pentagonal males exhibit relatively greater fecundity than females that mate with semi-oval males. This result is consistent with previous studies examining the fitness effects of spermatophores on female firefly fecundity. Rooney and Lewis (2002) documented a relative fecundity increase of 73% in triply vs singly mated female *Photinus ignitus* Fall.

Many nocturnally active fireflies use discrete pulses to locate their mates. In these species, males are the primary signalers (Lewis and Cratsley 2008). In *L. cerata*, although males are the primary signalers, male flashing behavior is significantly reduced in the absence of females. *Luciola cerata* has an HP communication system (Ohba and Yang 2003), and one of the characteristics of this system is that the female response delay time is constant (Ohba 1983). The results of this study support this previous finding since a relatively small standard error was observed in the female response delay time (Table 2).

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生態產業新趨勢——以阿里山賞螢產值及發展爲例

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摘　　要

整理阿里山地區螢火蟲資源調查結果共記錄 2 科 11 屬 42 種，依據成蟲出現的季節種類可規劃賞螢活動：春季為黑翅螢 (*Luciola cerata*)、大端黑螢 (*L. anceyi*)；夏季為端黑螢 (*L. praeusta*)、三節熠螢 (*L. trilucida*)；秋季為山窗螢 (*Pyocoelia praetexta*)、橙螢 (*Diaphanes citrinus*)；冬季則為神木螢 (*D. nubilus*)、鋸角雪螢 (*D. lampyroides*)。為發展阿里山螢火蟲生態產業，於 2001 年起進入阿里山地區教育民宿業者及社區民眾，講授螢火蟲相關課程，引導居民從觀察及瞭解螢火蟲之發光行為、生物學及生態學，體驗螢火蟲發光之美，進而達到保護螢火蟲棲地，營造賞螢之良好環境，使得賞螢活動成為該地區重要生物資源及生態導覽項目。為了瞭解當地民宿業者對於賞螢活動規劃行程及所獲得的產值，並建立當地民宿業者資料，自 2007 年 6 月至 2008 年 2 月止，以問卷成功訪問了 31 家民宿業者，結果得知業者經營賞螢活動平均 7.5 年，以春、夏季為主；導覽解說賞螢時段在晚上 6～9 點間，每晚一場。並根據結果推估阿里山地區民宿活動年營收 (不包含農特產品) 約為 9 億 3 仟 1 百萬元。賞螢季 (4 月至 6 月) 業者總營收約 52,654,560 元，約占全年營收之 28.67%；非賞螢季 (7 月至次年 3 月)業者總營收 131,011,920 元，約占全年營收之 71.33%；賞螢季的月營收約 17,551,520 元 (54%)，顯著高於非賞螢季之月營收 14,556,880 元 (46%) ($p = 0.023$, $\delta < 0.05$)，證實賞螢活動對於民宿及旅行業者所帶來的收益甚高。本研究亦建議對於螢火蟲生態產業中提高產值、提出經營管理與競爭力的方法，打造阿里山成為國際級賞螢區的新典範。

關鍵詞：螢火蟲、生態民宿、生態產業、阿里山地區。

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前　言

螢火蟲是重要的環境指標生物，人們透過對於螢火蟲及生態系的瞭解，體認到其對於維繫人類生命的重要性，進而維持與保護生態系的多樣性，以達到永續發展的目標 (Ho and Su, 2000)。我國鄰近的日本、泰國及馬來西亞等國家，皆積極推展螢火蟲之環境教育及生態民宿 (Ho and Yang, 2007)，不僅從保育的過程中，學習如何應用這些特殊的生態資源，在有系統的整合與規劃下，有效率的推出合適的遊程，期盼在生態的、深度的、教育的及體驗的民宿中讓遊客能瞭解大自然美景的內涵，進而保護環境與永續利用生物資源。

近十餘年來台灣的賞螢活動受到各方面的重視，此外國家公園 (Yang, 1996; Jeng *et al*., 1999a; Chang, *et al*., 2000)、國家森林遊樂區 (Ho, 2004)、國家風景區 (Ho, 2007)、各縣市 (Ho, 1998; Ho *et al*., 1998a, 2001, 2006; Chen, 2003) 及休閒農場 (Wu and Yang, 2008) 紛紛展開螢火蟲資源調查，不但使得螢火蟲分類學研究成果豐碩 (Lai *et al*., 1998; Jeng and Yang, 2003)，而且在螢火蟲發光行爲 (Ohba and Yang, 2002)、生活史相關研究 (Chen *et al*., 1998; Ho, 1998; Ho and Chiang, 2002; Ho and Huang, 2003; Ho *et al*., 2003) 及螢火蟲棲地特性與經營管理 (Yeh, 1999; Wu and Perng, 2007) 等基礎生物學上也頗有進展，加上棲地營造成功之範例介紹 (Ho and Chiang, 2002)，提供社區及一般民眾營造棲地生態之參考，保育與復育螢火蟲，而螢火蟲科普或生態推廣書籍紛紛問世 (Ho and Chiang, 1997; Ho and Jong, 1997; Yang, 1998; Ho *et al*., 2002b; Chen, 2003; Ho, 2007)，更使得一般社會大眾瞭解螢火蟲目前生存之危機，同時也喚醒社會大眾共同保育螢火蟲。此外，人工飼養技術之開發成功 (Chang, 1994; Chen and Chen, 1997; Ho and Chiang, 2002; Ho *et al*., 2006)，除了可在研究室中保存螢火蟲種源，也能夠整體開發及規劃螢火蟲資源。

任何利用直接或間接利用昆蟲本身或其產物之產業皆可視爲昆蟲生態產業之一部份生態產業，而生態產業更是繼經濟技術開發、高新技術產業開發發展的第 3 代產業。包含農業、居民區等的生態環境和生存狀況的一個有機系統。通過自然生態系統形成物流和能量的轉化，形成自然生態系統、人工生態系統、產業生態系統之間共生的網路 (Dong, 2009)。台灣昆蟲相關產業發跡甚早，主要爲昆蟲標本及蝴蝶加工品之外銷，在生態保育的觀念日盛後，由環境教育解說導覽、生態旅遊、昆蟲寵物飼養、天敵大量培育作生物防治害蟲等項目取而代之 (Yang and Ho, 2003)。而賞螢活動在逐年普及下，亦形成一股經濟產業熱潮。爲提昇台灣螢火蟲生態產業之內涵，Ho and Yang (2007) 與 Yang (2007) 曾論述日本的螢火蟲生態產業與保育，並介紹日本螢火蟲保育團體與螢火蟲博物館，探討螢火蟲生態產業及其成功的條件。近年來昆蟲的生態產業也不斷的推陳出新，在政府積極推展生態旅遊下，曾將 2001 年列爲生態旅遊年，生態旅遊是「生態產業」之一類別，也符合生態產業之在地性、環保、永續、綠色、生態性之精神。而賞螢活動的發展也結合生態旅遊，而展現新的風貌。

Ho (2006, 2007) 調查嘉義山區之螢火蟲資源，記錄 2 科 11 屬 42 種之多，而台灣產螢火蟲種類約 63 種 (私人通訊)，約佔 63%。且阿里山地區各月份皆有各種常見螢火蟲出現。故依據其景觀性可規劃賞螢活動的種類，春季爲黑翅螢、大端黑螢；夏季爲端黑螢、

三節熠螢；秋季為山窗螢、橙螢；冬季則為神木螢、鋸角雪螢。從 2001 起至 2008 間，曾進入阿里山地區，進行民宿業者及社區居民之生態研習活動共計 10 場次，受訓人數達 800 人次，教導社區居民認識、瞭解及保育螢火蟲，協助居民進行夜間的解說導覽服務。本研究希望能以阿里山螢火蟲生態產業規劃與落實，透過民宿業者社區居民共同來保護螢火蟲，推廣優質之生態民宿活動，進而達到環境的保育及建立永續經營的雙贏局面。但是台灣螢火蟲生態產業之發展及產值部分尚無文章具體論述，因此將以問卷方式調查阿里山地區民宿業者經營賞螢活動之經營現況，作為今後推廣台灣螢火蟲生態產業之範例，並提供民宿業者經營管理的方法及建議。

材料與方法

一、阿里山地區賞螢活動歷史與沿革

阿里山地區之賞螢活動歷史資料係採取質性研究方式，藉由網站資料瀏覽、文獻閱讀及在訪談民宿業者過程中所獲得之開放式訪談資料，經由編碼 (coding)，編寫故事軸線 (story line)，將網站、文獻暨開放式訪談資料彙整，整理出阿里山地區民宿業者辦理賞螢活動情形及發展之歷史背景。

二、阿里山地區民宿業者賞螢活動之經營現況暨產值估計

賞螢活動是具有商業價值的民宿經營項目之一，惟住宿價格、旅客人數等均由民宿業者與旅客雙方決定，故產值的估算不易；但為探討阿里山地區賞螢活動現況分析與產值，根據訪問民宿業者每月遊客數、住宿房間單價、用膳情形及解說導覽等情形，以賞螢季與非賞螢季的假日 (週五至週日) 及非假日 (週一至週四) 營業額進行分析，其中不含農產品之營收 (如山葵、茶葉、蔗糖、竹筍等)。自 2007 年 6 月起至 2008 年 2 月間，訪問了 31 家業者，調查範圍含蓋了阿里山地區的番路鄉 (3 家)、阿里山鄉 (9 家)、竹崎鄉 (5 家) 和梅山鄉 (14 家)，約佔阿里山地區民宿業者 20%，以初步推估阿里山地區螢火蟲生態產業經營的現況。本調查以封閉式問卷 (表一) 進行訪談。本問卷可區分為兩部分：第一部分為經營現狀及產值，第二部分為受訪者資料，第一部分共 21 題，第 7 題 (賞螢季之相關促銷活動) 之訪談結果作為阿里山地區民宿業者營業額估算之根據，而第 18 題之訪談結果為業者目前經營困難之依據，其餘題目皆為阿里山地區民宿業者對於賞螢活動經營現況之根據。訪談結果以 Microsoft Excel 進行整理及初步統計，並以 pair *t*-test 檢定非假日、假日、賞螢季、非賞螢季之營業額是否具統計之顯著差異。

結果與討論

一、阿里山賞螢的歷史與沿革

早期阿里山地區是以杉林和竹筍為最大宗產業，由於傳統農業沒落，逐漸以精緻農業取代；是故高山茶、山葵、愛玉、甜柿等特產成為新興的農產品。此外，當地擁有豐富的生態民宿資源，居民積極朝向生態民宿理念來經營與建構，發展生態民宿觀光，將部份高山農業轉型成休閒服務業。根據訪談資料 (梅瑞 1～梅瑞 8) 得知：「1970 年代阿里山瑞里地區是最熱門的登山路線之一，當時登山客黑夜裡看見閃閃發光的螢火蟲穿梭在樹林間或山谷間競舞，無不深受感動，不僅喚醒起遊客兒時追逐螢火蟲的記憶及對大自然的渴望，更帶動當地居民開始留意這些夜間發光的小昆蟲。當

表一　阿里山螢火蟲生態產業之市場價值評估問卷

Table 1.　The Questionnaire of firefly ecological industry at Mt. Ali area

第一部份一經營現狀

1.請問您已開業幾年？ 從　　　至　　　，共　　　年。

2.營業至今所投資額約：

□小於 1000 萬 □1000 萬~5000 萬 □5001 萬~1 億 □大於 1 億

□　　　萬元

3.員工人數：

自家人：　　　人　　　外聘員工：專職：　　　人、兼職　　　人

4.賞螢歷史沿革：□有辦理賞螢活動，至今已有　　　年

□沒有辦理賞螢活動

5.每年的「螢火蟲季」時間

春季是：　月～　月，種類有　、　、　、　、

夏季是：　月～　月，種類有　、　、　、　、

秋季是：　月～　月，種類有　、　、　、　、

冬季是：　月～　月，種類有　、　、　、　、

6.每年的「螢火蟲季」地點

春季是：

夏季是：

秋季是：

冬季是：

7.請問您是否在每年的「螢火蟲季」推出相關的促銷活動 (如住房優惠、螢火蟲專案)？

促銷活動時間是：　月～　月，活動名稱

螢火蟲季						非螢火蟲季					
假日			非假日			假日			非假日		
人數	條件	價錢	人數	條件	價錢	人數	條件	價錢	人數	條件	價錢

8.「螢火蟲季」是否提供螢火蟲導覽服務，□有，□沒有

一天幾個場次　　　次

一場導覽要多久時間　　　小時

導覽服務是否收費？

□住宿遊客沒有另外收費，□沒住宿遊客有收費，收費標準　　　元

導覽服務自行帶隊 □是，□否

一場次須要　　位解說員

解說員一次費用　　　元

9.依據您的觀察，當地螢火蟲數量是逐漸減少、增加或維持不變？

(1) □減少　主要原因

(2) □增加　主要原因

(3) □維持不變

10.螢火蟲季時是否曾經發生安全問題？如何解決？(可複選)

□跌倒 □蛇咬 □蜂螫 □其他意外

發生安全問題如何解決

11.是否爲遊客提供賞螢觀賞工具 (可複選)

□手電筒 □放大鏡 □紅色玻璃紙 □其他工具

表一　續
Table 1.　countied

12.爲遊客進行螢火蟲導覽服務之前，是否有提供其他服務？(可複選)
　□導覽之前解說 □摺頁 □其他資料
13.請問您主要是提供那些服務？(可複選)
　□住宿 □餐飲 □農特產品銷售 □生態導覽解說 □文化創意產品 □其他
14.除螢火蟲季之外，非螢火蟲季有無其他導覽服務？
　□動物生態　如：　　　　　　時間
　□植物生態　如：　　　　　　時間
　□文化　　　如：　　　　　　時間
　□其他　　　如：　　　　　　時間
15.文化創意產品主要爲何種？
　□衣服 □杯子 □扇子 □手提燈 □手機吊飾 □玩偶 □手工藝品 □其他
16.目前貴單位有無接受政府協助、輔導？
　中央政府 □有，□沒有
　地方政府 □有，□沒有
17.貴場所對於螢火蟲季活動或螢火蟲棲地有何投資？
　□棲地鋤草　金額　　　　元
　□活動宣傳　金額　　　　元
　□印刷螢火蟲相關資料　金額　　　　元
18.目前在經營上面對哪些困難？
19.如需政府輔導，需要哪方面的協助？
　□報章雜誌、平面媒體
　□電子媒體宣傳、網路
　□安排螢火蟲解說人員教育課程
　□提供摺頁相關教材支援螢火蟲導覽
20.螢火蟲季貴場所舉辦的各種活動對於貴場所的利潤是否有提升效果？
　□有
　□沒有原因
21.您認爲螢火蟲資源之永續利用及螢火蟲季的舉辦對於貴場所之經營是否有正面之幫助？
　□有
　□沒有　原因

第二部分一受訪者資料
店名：
主要營業項目：
聯絡人及聯絡方式：姓名　　　　電話：　　　　傳真：　　　　e-mail:

時瑞里地區的若蘭山莊首開風氣之先，發現螢火蟲的數量極多，具良好之景觀性，便開始著手棲地的保護，從人工除草，提高棲地環境濕度，增加幼蟲食物等經營管理工作，民宿業者用心投入棲地保育工作，使得螢火蟲保育更具成效」。1989 年起當地首推螢火蟲生態導覽活動後，引起各方的矚目，成爲全台最具代表性、指標性的賞螢地點之一；而早期多爲小規模民宿，服務項目以住宿、餐飲、農特產品爲主要經濟收入來源，由於阿里山地區高山環繞，自然景觀發達及豐富的動植物資源，近年來業者經營方向逐漸以生態、風景導覽解說爲

重點，且受到竹崎鄉瑞里村若蘭山莊經營賞螢活動，成功地提高遊客量之影響，逐漸成為熱門的生態民宿主要行程之一。

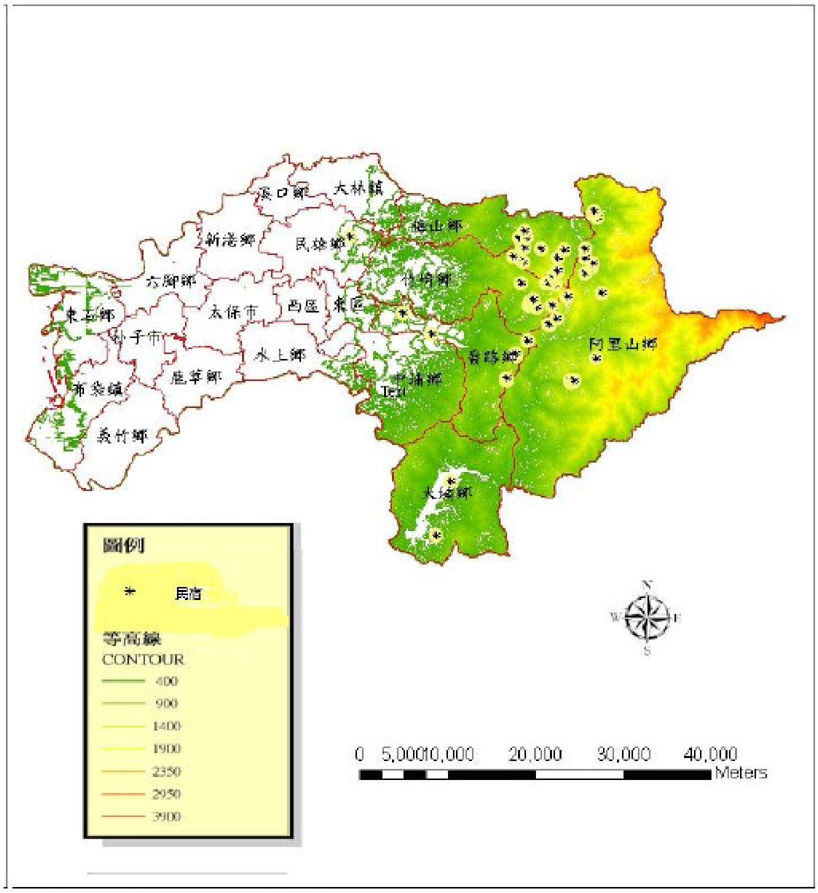
自 2003 年起每年於 4、5 月螢火蟲發生季節，由阿里山國家風景區管理處、嘉義縣政府及嘉義林區管理處共同舉辦「與螢共舞」系列活動，聯結櫻花季之後的民宿淡季，以 4 月至 6 月「螢火蟲生態民宿」作為該區民宿之主軸，並藉助平面媒體與電子媒體之行銷來推廣與宣導，結合社區與民宿業者共同努力推動，來增加遊客夜間的自然體驗活動，以延長遊客留宿的時間，提高山區的生態民宿經濟收入。

二、阿里山經營賞螢活動的民宿現況調查

據訪談調查得知，阿里山地區民宿業者大多由夫婦經營，員工人數在 2~12 人之間，而且員工多為親戚或來自當地的居民，員工收入以打零工方式計資，除了平日的打掃工作外，也須充當導覽解說員之工作。開業最長者 60 年，最短 3 年，平均 11 年。投資金額少於 1,000 萬元者共 10 家，1,000 萬~5,000 萬共 8 家，另 13 家業者並無填寫投資金額，而 18 家業者平均投資金額約 1,611 萬元。

根據 2008 年嘉義縣觀光民宿網合法旅社民宿資料內容詳載 (http://www.tbocc.gov.tw)，梅山鄉旅社與民宿 62 家，其中有賞螢活動者 6 家，佔 9.6%。竹崎鄉旅社與民宿 63 家，其中有賞螢活動者 14 家，佔 22.2%。阿里山鄉旅社與民宿 63 家，其中有賞螢活動者 13 家，佔 20.6%。三鄉合計有 188 家民宿，其中有賞螢活動者 33 家，佔 18%。然而在訪談過程中瞭解目前民宿業者只要遊客有需求，幾乎都有帶團賞螢。整體而言，賞螢活動在阿里山地區是主流的生態導覽項目。

阿里山地區經營賞螢活動之時間平均約 7.5 年，全數以春、夏季為主，而春季種類以黑翅螢及大端黑螢居多；春季賞螢時段以晚上 6~9 點為主，民宿業者安排之賞螢旅程為二天一夜之套裝行程，只有一場夜間導覽，沒有另外再收取導覽解說費用者居多；僅有 1 家業者有進行收費。賞螢的地點大多以附近步道進行，較無安全上的顧慮，據問卷結果，僅 1 家業者有遊客被蛇咬，另 2 家業者有遊客在賞螢過程中跌倒，各家民宿業者之賞螢導覽歷時約 1.5~2.0 小時後結束，但也有在自家私有地上辦理賞螢活動，如若蘭山莊。在賞螢前，通常業者召集遊客作行前說明，或是播放錄影帶及電子多媒體，介紹螢火蟲生態與保育，並提醒遊客必要的賞螢規範及注意事項。當說明完後，再由業者帶到固定的地點進行賞螢活動，有 14 家民宿業者會提供必要的賞螢工具，如紅色的玻璃紙或 LED 燈等，減少在棲地間的光害，影響螢火蟲的發光與賞螢的品質；而其餘業者則需遊客自備賞螢工具；由於阿里山地區之螢火蟲資源調查雖有定性之種類調查結果，但缺乏定量之螢火蟲族群數量資料，故藉由問卷第 9 題，讓民宿業者自行估算阿里山地區螢火蟲數量變化情況，此調查結果雖無法表現阿里山地區螢火蟲數量變化之精確情況，但由於這些民宿業者久居阿里山地區，故仍能藉由其日常觀察或賞螢過程中所觀察到之螢火蟲數量，顯示阿里山地區開始有民宿業者舉辦賞螢活動之後，螢火蟲數量的變化趨勢，據問卷結果顯示，共有 18 家業者表示螢火蟲數量不變，9 家業者表示增加，4 家業者表示減少，據 9 家表示螢火蟲數量增加之業者，其認為螢火蟲增加之原因為農藥施用量減少，而 4 家表示螢火蟲數量減少的原因為住宅區開發增加及氣候改變。

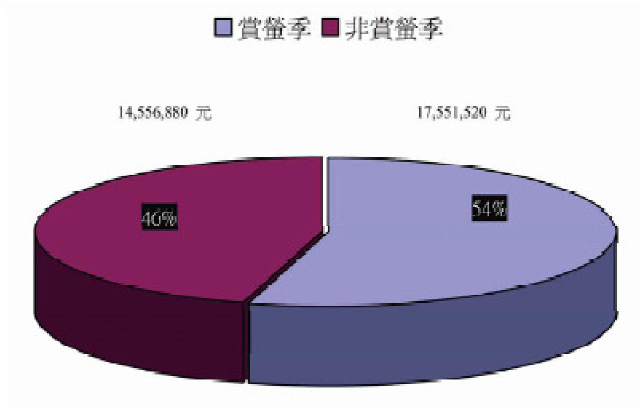


圖一　阿里山地區 31 家受訪民宿業者之分布圖。
Fig. 1.　The map of the 31 B&B places in the Mt. Ali area.

三、實螢活動所創造的產值調查

(一) 阿里山地區民宿業者之營收

2007 年 6 月至 2008 年 2 月間成功地訪問了 31 家民宿業者，訪問調查結果得知，其全年營收約 186,245,280 元，初步推估阿里山地區民宿活動年營收約 931,000,000 元 (不包含農特產品)。在阿里山地區的民宿業者主要為民宿及飯店，無具規模



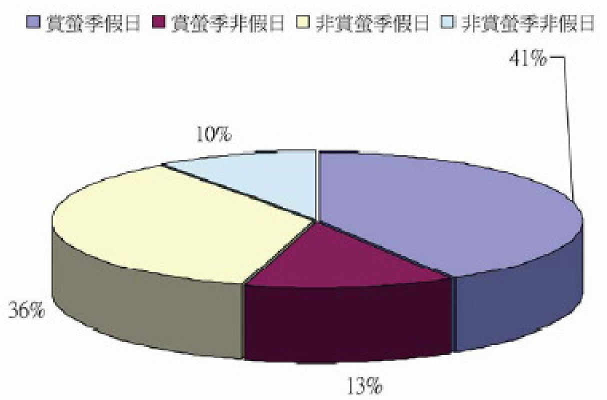
圖二 阿里山地區賞螢季與非賞螢季民宿業者營收之比較，具顯著差異 (p = 0.023, $\delta < 0.05$, paired t-test)。
Fig. 2. Comparison of the output value of the ecotourism in the Mt. Ali area during the firefly watching season and the remainder of the year (p = 0.023, $\delta < 0.05$, paired t-test).

的商業大飯店或商務旅館。遊客多數以家庭為主的散客為大宗。根據問卷結果分析，比較假日及非假日月營收情況，假日月營收約 24,948,480 元，顯著高於非假日之月營收約 7,159,920 元 (p = 0.002, $\delta < 0.05$, paired t-test)，在民宿經營中主要為假日的民宿活動居多。當地的民宿業者非假日以務農為主，經營農產為大宗；假日改以經營民宿為主之服務業，以民宿型態經營居多，是小眾民宿型態，業者可搭配平日的農務工作，販賣與直銷當地出產之新鮮美味之農產品，生活與工作安排上較具有彈性。

(二) 賞螢季及非賞螢季月營收之比較

根據問卷結果分析比較賞螢季 (4 月至 6 月) 及非賞螢季 (7 月至次年 3 月) 之月營收情況，賞螢季業者總營收約 52,654,560 元，約占全年營收之 28.67%。非賞螢季業者總營收 131,011,920 元，約占全年營收之 71.33%。賞螢季的月營收約 17,551,520 元 (54%)，顯著高於非賞螢季之月營收 14,556,880 元 (46%) (p = 0.023, $\delta < 0.05$, paired t-test，圖二)。賞螢季的假日月營收 13,432,000 元，也明顯高於賞螢季非假日月營收 4,119,520 元，假日之月營收約為非假日的 3.5 倍 (p = 0.027, $\delta < 0.05$, paired t-test，圖三)。比較賞螢季節與非賞螢季節的營收，在 3 個月春季賞螢活動的營收，佔全年營收的 28.5%，這是相當高的比例。賞春節連續假期之後的 4 月至 6 月期間原本是民宿市場的淡季，藉由賞螢活動的舉辦及促銷，吸引較多的遊客上山賞螢，進而提升民宿之住房率，並可促銷春天的農特產品，如春茶、春筍及梅子等，因此民宿業者賞螢季的營收逐漸成為阿里山地區的民眾重要的經濟來源之一。

(三) 賞螢季假日及非賞螢季假日月營收之比較



圖三　阿里山地區賞螢季假日、賞螢季非假日、非賞螢季假日及非賞螢季非假日民宿業者營收之比較。
Fig. 3. A comparison of the output value of the ecotourism in the Mt. Ali area (holidays vs. non-holidays during the firefly-watching and the non firefly-watching season).

分析問卷結果，賞螢季假日業者營收 13,432,000 元，也高於非賞螢季假日營收 11,516,480 元 ($p = 0.002$, $\delta < 0.05$, paired t-test，圖三)，從訪談中得知，賞螢期間的假日住房率是 100%，而非賞螢季假日則略低，為 95%。從營收得知，旅客多數喜歡利用假日到阿里山民宿，這是較固定的山區民宿型態。

(四) 賞螢季非假日及非賞螢季非假日月營收之比較

分析比較賞螢季及非賞螢季非假日之月營收情況，賞螢季非假日營收 4,119,520 元，顯著高於非賞螢季非假日營收 3,040,400 元 ($p = 0.028$, $\delta < 0.05$, paired t-test，圖三)。賞螢季非假日住房率雖低，亦高於非賞螢季非假日的住房率。不過賞螢活動主要為家庭及年青人為導向的活動，因此還是假日較受歡迎。當地業者認為目前面臨經營困難點為「非假日的遊客量較少」，是故提升非假日住房率，才是解決此問題的根本之道。其方法包括加強非假日的促銷活動及媒體宣傳、提高民宿品質、開拓國際市場並接受國外遊客網路訂房等。

(五) 賞螢季、暑寒假之月營收比較

據問卷結果分析比較賞螢季及寒暑假之營收情況，賞螢季月營收約為 17,650,320 元，顯著高於寒暑假之 14,810,480 元 ($p = 0.005$, $\delta < 0.05$, paired t-test)，顯示寒暑假與遊客量增加無關，但賞螢季因有舉辦賞螢活動，反能增加遊客數，提高營業額。

四、阿里山地區民宿業者之經營面臨問題

(一) 培訓解說導覽人員或提供解說素材：從問卷結果得知，螢火蟲生態解說員都由民宿主人擔任，而民宿主人對於螢火蟲生態之認識多為自身觀察結果，故解說內容較

少；又因經費之故，無其他解說員支援，造成業者認爲當地缺少解說人員，因此螢火蟲生態導覽員的培訓活動仍需持續舉辦。此外建議阿里山國家風景區管理處及嘉義林區管理處需加強招募志工，特別在賞螢季節中，投入定點的解說導覽，提昇賞螢之品質與內涵；而目前螢火蟲解說導覽光碟皆過於老舊，因此有必要將阿里山賞螢發展歷史及螢火蟲景觀作一完整介紹，除教育社會大眾之外，也可作爲生態導覽之教材。

(二) 加強媒體的宣傳及摺頁製作：透過平面或電子媒體將螢火蟲發光的景觀或將簡明之生物學背景資料介紹給社會大眾。建議由地方政府或主管機關能夠編列足夠廣告預算，配合賞螢季活動的規劃及配套，行銷賞螢活動，至於目前螢火蟲宣傳品內容過於專業，在美編及出版時，多應擬人化，以更口語的表達螢火蟲的意境與情感，以通俗性教育爲主要導向。

(三) 推廣秋冬賞螢活動：阿里山區四季皆有不同種類之螢火蟲，故建議除可觀賞春季賞螢活動外，秋冬季之窗螢屬的山窗螢及短角窗螢屬的神木螢、鋸角雪螢也值得欣賞，其發光特性與春季熠螢屬種類完全不同；當地秋冬螢火蟲雖然經過調查研究(Ho, 2007)，業者亦知秋冬可賞螢，然秋冬賞螢需要在海拔 2,000 公尺高山進行，恐遊客禦寒及體力無法負擔，故未大力推廣。此亦需要政府單位及民宿業者共同推動，才能提升產值。

(四) 參與國際生態旅遊行銷：遴選阿里山國家風景區內具有良好形象之生態社區，經專家評選其社區螢火蟲棲地營造、套裝行程、螢火蟲創意商品、環境品質之維護管理、設計體驗活動等項目，凡達到標準者，由阿里山國家風景區管理處推薦並積極協助參加亞太地區的國際旅遊展覽，不僅可將台灣螢火蟲發光之美行銷到國際上，並讓經營螢火蟲生態產業的休閒業者與國外人士交流與觀摩的機會，來提昇社區之生態旅遊品質。

五、阿里山國家風景區螢火蟲之永續經營與利用

阿里山國家風景區的生態旅遊之發展與一般性的觀光旅遊不同，因此在規劃上應採取可控制的選擇模式，生態旅遊有經濟、社會及環境的目標，而這些目標的優先順序，需要不斷的討論與調整，經由民宿業者的努力以赴才能達成。在社區參與上，世界各地自然保護區發展證明只有當地社區對於自然環境保育表示支持態度時，自然保育的工作才能夠順利推行。而當地社區能否從自然保育中獲得經濟利益與當地社區居民對保護的物種或環境的態度有密切關係。在結合社區經濟發展及自然保育的前提下，提高社區居民的國民所得，而得到利益的居民願意投身自然保育工作，螢火蟲棲地臨近區內的事務才能夠受到居民的支持與協助，社區居民透過保育螢火蟲棲地，營造良好的賞螢環境，吸引遊客前來賞螢，創造社區居民的利益，以達永續經營目的。

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