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Morphological Redescription and Population Fluctuation of Frog Flies, *Caiusa violacea* Séguy (Diptera: Calliphoridae), in Taiwan

Yu-Zen Huang[1,2]*, Shiuh-Feng Shiao[2]

[1] Graduate School of Integrated Sciences for Global Society, Kyushu University, Fukuoka, Japan
[2] Department of Entomology, National Taiwan University, Taipei, Taiwan
* Corresponding email: b99612028@ntu.edu.tw

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ABSTRACT

The frog fly *Caiusa violacea* Séguy is a dipteran species whose larvae develop in amphibian egg clutches which they then consume. In Taiwan, frog flies lay eggs on the foam nests of tree frogs, such as *Polypedates braueri*, *Rhacophorus prasinatus*, *R. aurantiventris*, and *R. moltrechti*. This species was misidentified as *C. coomani* Séguy but was later confirmed to be *C. violacea* Séguy, the only species of this genus recorded in Taiwan. This study aimed to determine the population fluctuation of *C. violacea* and its host connections in northern Taiwan. Samples were collected every two weeks from study sites at the Taipei Zoo. The results showed that the population size of *C. violacea* is larger between June and October, when the temperature is higher and rainfall is abundant. This period is approximately the breeding season of *P. braueri*. Because of the seasonal coincidence of the emergence of flies and the reproduction of frogs, we conclude that *P. braueri* is the major host of *C. violacea* in northern Taiwan. In addition, we provide a morphological redescription of *C. violacea* to facilitate identification.

Key words: Frog flies, *Caiusa*, tree frog, population dynamics, parasitoid

Introduction

Most frogs lay their eggs in water which are typically preyed upon by aquatic predators such as fishes, arthropods, and other aquatic invertebrates. By contrast, tree frogs build foam nests. A foam nest is composed of cloacal secretions and gelatinous mucopolysaccharide from parent frogs (Villa, 1978; Vitt and Caldwell, 2008). The foam nest is built away from water, thus protecting the eggs from aquatic predators but making them vulnerable to terrestrial predators such as ants, wasps, beetles, and flies (Villa *et al.*, 1982).

Frog flies are dipterans whose larvae develop in amphibian egg clutches, particularly frog eggs (Villa, 1980). Frog flies belong to many families, such as Calliphoridae, Chironomidae, Drosophilidae, Ephydridae, Phoridae, and Psychodidae. The relationships between hosts and flies are diverse, and some flies accidentally inhabit the foam nests of decomposed egg clutches, with dead embryos, or detritus present in the nests (Bokermann, 1957; Villa, 1977; Villa, 1980; Villa *et al.*, 1982; Downie *et al.*, 1995; Menin and Giaretta, 2003).

Among frog flies, obligate frog flies live in and feed on frog eggs for larval development; in some cases, obligate frog flies may prey upon only one or some closely related frog species (Villa, 1980). These frog flies are considered parasitoid flies by Villa (1980), Downie *et al.* (1995), Lin *et al.* (2000), and Lue and Lin (2000). However, in contrast to the larvae of typical parasitoid insects, the larvae of frog flies consume more than one individual, and the hosts are not invertebrates. This special relationship between obligate frog flies and frogs has rarely been discussed.

Frog flies in Taiwan were misidentified as *Caiusa coomani* Séguy by Lue and Lin (2000). Rognes (2011) dissected the lectotype of *C. coomani* and observed that the male genitalia were different from those in the pictures in the keys reported by Fan (1992), which were adopted by Lue and Lin (2000). Because of the high intraspecific variation in external characteristics and unknown structure of the male genitalia of most species of the genus *Caiusa*, the frog fly species in Taiwan remained classified as *Caiusa* sp. for several years (Yang *et al.*, 2014). Subsequently, Rognes (2015) revised the genus *Caiusa* and suggested that *C. violacea* Séguy is the only *Caiusa* species in Taiwan.

The larvae of *C. violacea* feed on the foam nests of *Polypedates leucomystax* in China and on those of *Chiromantis nongkhorensis* in Thailand (Rognes, 2015). In Taiwan, four species of tree frogs, *P. braueri*, *Rhacophorus aurantiventris*, *R. moltrechti*, and *R. prasinatus*, were recorded as being preyed upon by this maggot species (Lue and Lin, 2000). Tree frogs build foam nests only in the breeding season, making foam nests a time-limited resource. Therefore, the effect of the frog breeding season on frog flies should be investigated. Chen (1992) reported that *R. prasinatus* could be infested by frog flies between February and November; and moreover, all the foam nests they collected were infested between May and August. However, the infection rate of *P. braueri* was not simultaneously recorded. Because the dynamics of frog fly populations remain unknown, we could not determine the effects of foam nests and climatic factors on frog flies. Therefore, in this study, we recorded the yearly population fluctuation of *C. violacea* and analyzed the correlation between temperature, rainfall and size of the frog fly population.

Materials and Methods

This study was conducted using bait traps for collecting *C. violacea*; the traps were composed of plastic cans 11.5 cm in diameter and 21.0 cm in height. Pork liver was used as the bait. Samples were collected approximately every two weeks between May 2013 and June 2014.

The study site was located at the physical exercise field of Taipei Zoo, Wenshan District, Taipei City. Taipei zoo is a zoological garden with a secondary forest at an altitude of 102 m. Temperature was recorded once an hour by using temperature data loggers (Onset HOBO® U23). The rainfall data were acquired from the Wenshan automatic weather station, which is 1.85 km from the study site. Moreover, data on the association between the number of flies and rainfall were analyzed through linear regression by using R (ver. 3.1.0) and input using the chron package to include a temporal description. Terminology used here is based mainly on McAlpine *et al*. (1981) and Sinclair (2000).

Results

Redescription of *Caiusa violacea* Séguy, 1925 (Fig. 1)

Holotype female, Cambodia (MNHN), by monotypy.

Caiusa dubiosa Villeneuve, 1927: 392.

Phumosia indica: James 1977: 537.

Phumosia indica: Kurahashi 1989: 709.

Caiusa indica: Feng *et al*. 1998: 1454.

Caiusa testacea: Feng *et al*. 1998: 1454.

Phumosia indica: Lin & Chen 1999: 115.

Caiusa indica: Yang *et al*. 2014: 96.

Caiusa testacea: Yang *et al*. 2014: 96 [citing Hennig (1941: 180)].

Caiusa sp.: Yang *et al*. 2014: 96.

Complete synonymies see Rognes, 2015: 61-62.

Material examined. 2♂, NEW TAIPEI CITY: Xindian Dist.: Sikanshui 500 m, 4-IX-2013, Y. Z. Huang. 3♂, TAIPEI CITY: Beitou Dist.: Yangmingshan National Park, Jhuzihhu

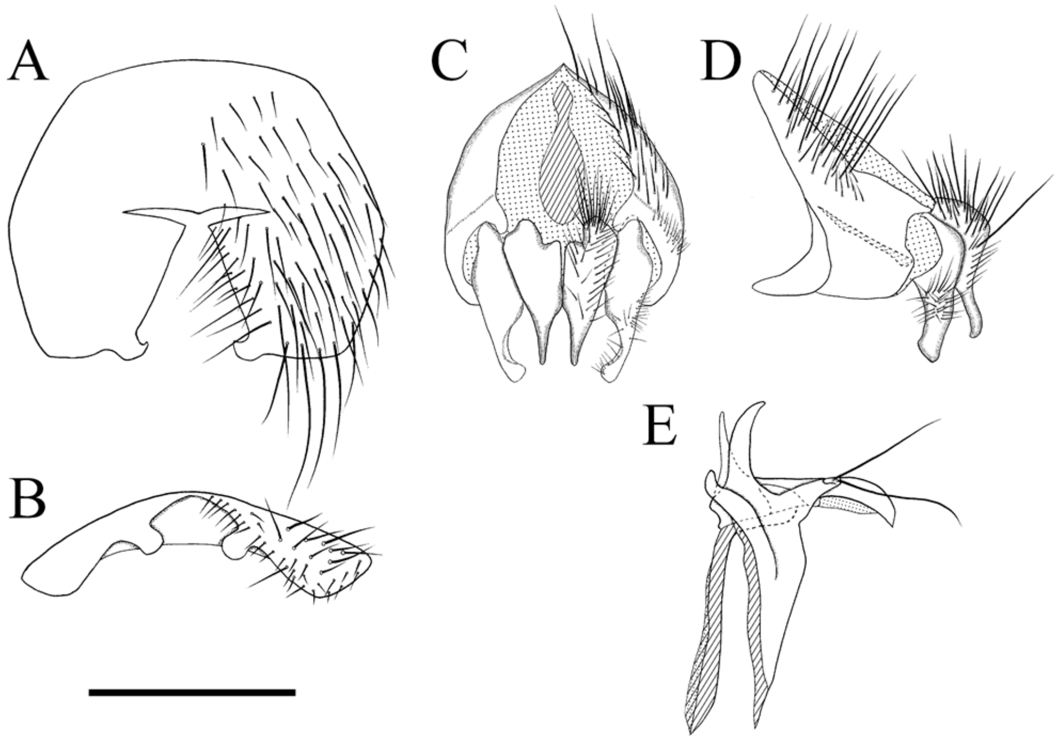

Fig. 1. Male hypopygium of *Caiusa violacea*. (A) Ventral and (B) anterior views of the fifth sternum; (C) dorsal and (D) lateral views of the epandrium, cercus, and surstylus; and (E) lateral view of the hypandrium, pregonites, postgonites, and aedeagus. Scale bar = 0.5 mm.

670 m, 27-VI-2014, Y. Z. Huang. 5♂9♀, TAIPEI CITY: Wenshan Dist.: Taipei Zoo 102 m, VII-2015, L. C. Huang. (All specimens deposited in the Department of Entomology, National Taiwan University.)

Male. Head: interfrontal area black; parafacial reddish; face and gena densely greyish pollinose; anterior portion of gena brown; epistoma brown; occiput greyish white pollinose at upper portion and white pollinose at lower portion; antenna with scape and pedicel yellow, 1st flagellomere black, inside yellowish narrowly on base; palpus yellow. Frons at vertex / head width, 0.13-0.14; parafacial strongly narrowed below; gena / eye height, 0.06-0.09; occiput rather flattened; inner vertical seta / eye height, 0.15-0.16; outer vertical seta indistinct or absent; ocellar seta / inner vertical seta, ca. 0.67; 4-7 frontal setae, lowest one inserted level with base of scape; vibrissa insertion above lower margin of face. Eyes bare; antenna with pedicel 0.25 × as long as 1st flagellamere; 1st flagellamere 0.33 × as wide as long; arista plumose. Palpus nearly cylindrical, subequal in length to 1st flagellomere.

Thorax: thorax black in ground color; dorsum with dense black pollinosity; pleuron thinly yellowish black pollinose; dorsum of prescutum and scutum with 1 black longitudinal vitta and 2 thinner yellow vittae; 1-2 presutural and 1-2 postsutural acrostichal setae; 2 presutural and 4 postsutural dorsocentral setae; 1 presutural and 3 postsutural intra-alar setae; 3 postpronotal setae in straight line; 1 anterior and 1 posterior katepisternal setae; basal scutellar seta 1.09 × as long as scutellum, subapical scutellar seta subequal in length to basal one, apical scutellar setae convergent; distance between 2 subapical scutellar setae about 0.75 × as long as that between basal and subapical ones of same side.

Wing: wing hyaline; veins brown; calypter pale whitish yellow; halter pale yellow. Second costal section about 0.5 × as long as 3rd, and subequal in length to 4th; length of vein M from dm-cu crossvein to its bend about 0.56 × as long as that from the bend to apex of vein M, and about 2.25 × as long as length between the bend and wing margin; dm-cu crossvein weakly curved; ultimate section of vein CuA1 about 0.5 × as long as dm-cu crossvein. Second costal section with fine hairs on ventral side; 4th costal section setulose on ventral basal 1/2; R_{4+5} setulose on dorsal base 7/12.

Legs: legs yellow in ground color; 4th and 5th tarsomere black; pulvilli pale whitish yellow. Fore tibia with 3 anterodorsal, 1 posterior, 2 preapical dorsal and 1 preapical posterior setae; mid tibia with 1 anterodorsal, 3 posterior, 1 ventral, 2 preapical dorsal, 1 preapical posteroventral and 2 apical ventral setae; hind tibia with 3 anterodorsal, 2 posterior, 2 ventral setae, 2 preapical dorsal and 1 apical anteroventral setae.

Abdomen: Syntergite 1+2 and anterior of 3rd tergite yellow; posterior margin of 3rd tergite, and 4th and 5th terga metallic blackish brown. Dorsum and venter densely clothed with black pollinosity. Abdomen subequal in length to length of thorax. No discal or marginal seta on syntergite 1+2 to 5th terga.

Male genitalia: Surstylus clearly longer than cerci, curved inside at apical 1/4 in dorsal view, rather straight and broad in lateral view; cerci widely separated from each other at middle in dorsal view, slightly curved in lateral view; pregonite strongly curved apically outward at apex with 2 long strong hairs.

Female. Head: frontal vitta dark brown to black; parafrontal white, silver-white pollinose, parafacial silver-white. Frons at vertex / head width, 0.27-0.29; frontal vitta 2× as wide as parafrontal; 7-9 frontal setae; 1 reclinate orbital seta; 2 proclinate orbital setae; parafacial bare; 1 inner and 1 outer vertical seta. Otherwise same as in male.

Body Length. 5.00-7.25 mm.

Bionomics. Adults are frequent flower visitors. Larvae feed on foam nest of *Polypedates braueri*, *Rhacophorus prasinatus*, *R. aurantiventris* and *R. moltrechti* in Taiwan.

Distribution. Taiwan, Cambodia, China (Guangdong, Xishuangbanna), Laos, Malaysia (West Malaya, Sabah), Thailand and Vietnam.

Population Fluctuation

Figure 2A shows the population fluctuation of *C. violacea* from 2013 to 2014. In this study, a total of 90 flies, 26 males and 64 females were collected, and 86.7% (78/90) of the flies were collected between June and October. The number of females was higher than that of males on all collection dates. Figure 2A shows 4 peaks (June 7; July 19; September 13 and 27; and October 30) of fly emergence. A similar pattern of rainfall with 3 peaks (May 24, July 5, and August 30) is shown in Fig. 2B.

Based on the results of a linear regression of the association between the number of flies and the rainfall two weeks previously, when the temperatures were above 19°C (P = .011), our data also demonstrated a positive association between the number of flies and the rainfall two weeks previously at temperatures above 19°C.

Discussion

Six Taiwanese species of tree frogs that build a foam nest: *P. braueri*, *R. arvalis*, *R. aurantiventris*, *R. moltrechti*, *R. prasinatus* and *R. taipeianus*. *P. braueri*, *R. aurantiventris*, *R. moltrechti* and *R. prasinatus* were recorded as hosts of *C. violacea* (Lue and Lin, 2000). In addition, *P. braueri* and *R. prasinatus* were recorded to be hosts of *C. violacea* at Taipei Zoo (Chen and Tsau, 2004).

The breeding season of *P. braueri* is from May to September at altitudes below 500 m in northern Taiwan (Lu and Chen, 2012). By contrast, *R. prasinatus* can breed throughout the year, but builds more foam nests in March and from September to November (Chen, 1992). The population size of *C. violacea* was expected to be larger not only during the summer but also in both spring and autumn. However, the population size of *C. violacea* was lower from June to October, overlapping about four months with the breading season of *P. braueri*, but overlapping only two months with the breading season of *R. prasinatus*. Similarly, Lue and Lin (2000) indicated that the foam nest of *P. braueri* was the most severely infested one (55%) compared to that of the other frog species. The large overlap of the breeding season of *P. braueri* with the time of the fly population growth suggest that *P. braueri* is the main host of *C. violacea* in northern Taiwan.

The larger fly population in the summer suggests that temperature influences the size of the fly population. Savage *et al.* (2004) reported that within a particular range, the population of invertebrates can increase with the temperature. In a field survey of the oriental latrine fly (*Chrysomya megacephala* (Fabricius]), a positive correlation was observed between temperature and the number of flies collected

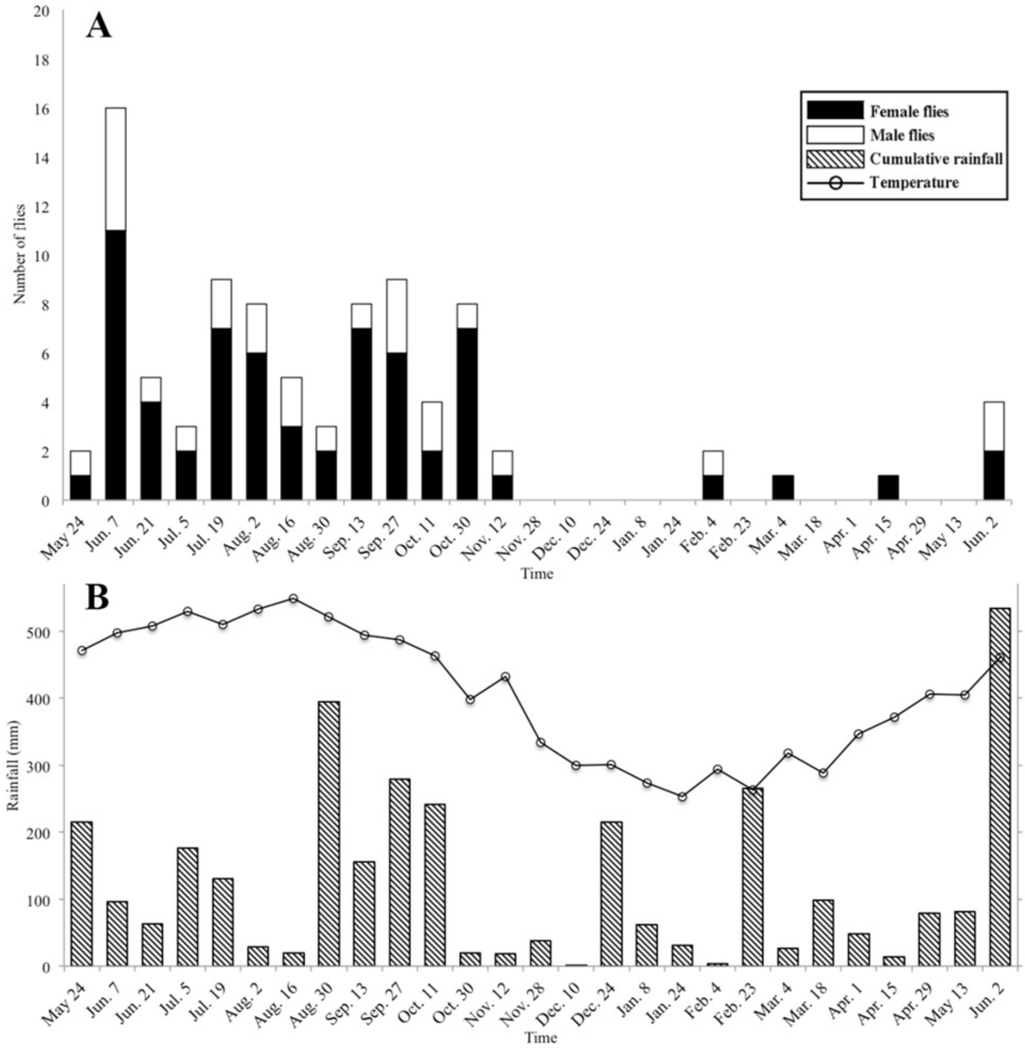

Fig. 2. Population fluctuation of *Caiusa violacea* from May 2013 to June 2014 at Taipei Zoo. (A) Total number of collected flies. The black and white bars show the number of female and male flies, respectively. (B) Data on temperature and cumulative rainfall at Taipei Zoo from May 2013 to June 2014. The bar chart represents temperature, whereas the line graph represents the cumulative rainfall. Data for December 10, 2013 were missing because the traps were destroyed that day.

(Ngoen-Klan *et al.*, 2011). In our study, more than 95% of the flies were caught from June to October, and the average temperature was 25.0°C. On the other hand, in the other months, only 4 flies were collected, representing about 5% of all flies collected, and the average temperature was 16.4°C. In addition, the number of female flies was always higher than that of males on all collection dates. This demonstrated that female flies were more frequently attracted to the traps, possibly because they require protein for ovary development (Browne and Gerwen, 1992).

Although a high temperature was associated with a larger population size of *C. violacea* prevailed between June and October, the number of flies still fluctuated during these five months. The rainfall also contributed to the population fluctuation. As shown in the results, the number of flies increased with the rainfall when the temperature was above 19°C. In addition, as shown in Fig. 2, the rainfall increased on May 24, and the number of flies increased two weeks later (June 7). This two-week delay may be the developmental time of *C. violacea*, whose life cycle from egg to adult takes approximately 12 days (Lue and Lin, 2000). The number of foam nests is highly correlated with rainfall; thus it can be assumed that tree frogs built their foam nests immediately after the rain and then were preyed upon by *C. violacea* (Chen, 1992; Lu and

Chen, 2012). Approximately two weeks after the rain, flies emerged and were collected. Although we did not record the number of foam nests, the number of flies collected may be affected by the number of foam nests, which is associated with rainfall. Further studies on recording the rainfall, number of foam nests and number of flies from June to October would be useful to learn their direct relationships. On the other hand, the correlation between rainfall and the number of foam nests has been observed before (Chen, 1992; Lu and Chen, 2012), and therefore it would be interesting to find out if there is a positive correlation between rainfall and the number of flies.

In conclusion, both temperature and rainfall can influence the population size of *C. violacea*. The fly population increases only under the two conditions of high temperature and abundant rainfall. Consequently, only a few flies nearly were collected in winter which is usually cold and dry. Previous studies have shown that none of the foam nests of *R. prasinatus* were attacked by frog flies in December and January (Chen, 1992). However, some foam nests would be required for frog flies to maintain their population lineage in winter, or maybe the flies have adopted other strategies to survive during the winter months. In Yangmingshan National Park in Taipei City, there are no hosts available for *C. violacea* between September and February (Yang *et al.*, 2012), and the lifespan of adult flies is approximately two months in the laboratory (personal observation). It would be reasonable to assume that frog flies are absent in the park since they cannot maintain their population during winter. However, three male flies were collected by sweeping on June 27, 2014. Thus, the strategies used by *C. violacea* to overwinter warrants further investigation. It remains unknown whether the flies can enter diapause as pupae or migrate to other habitats having more foam nests.

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臺灣蛙蠅-紫絳蠅（雙翅目：麗蠅科）形態重新描述與族群數量波動調查

黃悠然 [1,2*]、蕭旭峰 [2]

[1] 九州大學大學院地球社會統合科學府　744 Motooka, Nishi-ku, Fukuoka, Japan

[2] 國立臺灣大學昆蟲學系　10617 臺北市大安區羅斯福路四段 1 號

* 通訊作者 email: b99612028@ntu.edu.tw

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摘　　要

蛙蠅為幼蟲期於兩棲類卵塊中生長並取食其卵的雙翅目昆蟲。已知台灣的蛙蠅寄主有布氏樹蛙、翡翠樹蛙、橙腹樹蛙和莫氏樹蛙。台灣的蛙蠅曾被誤鑑定為印度阜蠅，但後來被確認為紫絳蠅，也是台灣目前唯一紀錄的蛙蠅種類。本研究進行了紫絳蠅的一年間族群波動調查。研究進行期間，每兩星期由台北市立動物園內樣區採取樣本。結果顯示，紫絳蠅族群在六月至十月間達高峰，與高氣溫和高降雨量有關。由高峰時間與樹蛙繁殖期推測，紫絳蠅在台灣北部低海拔地區的主要寄主應為布氏樹蛙。當溫度高於攝氏 19 度時，族群數量與兩週前的雨量顯著相關，顯示雨量為紫絳蠅數量波動之重要影響因子。

關鍵詞：蛙蠅、紫絳蠅、族群波動、樹蛙、卵泡