RESEARCH ARTICLE

Distribution, development biology and behavior of *Dacus persicus* associated with *Calotropis gigantea* in Sri Lanka

W.P.S.N. Wijeweera*, K.A.D.W. Senaratne and K. Dhileepan

Mating pair of *D. persicus*

Oviposition of *D. persicus*

Eggs of *D. persicus*

Larvae of *D. persicus*

Papae of *D. persicus*

Newly emerged *D. persicus*

Highlights

- *Dacus persicus* is a highly destructive monophagous insect pest of *Calotropis gigantea* in Sri Lanka.
- It is distributed in six out of nine provinces of Sri Lanka.
- Only larval stages of *D. persicus* feed on *C. gigantea*.
- *D. persicus* larva completely (100%) feed on seeds and highly influence on Calotropis reproduction.
- The number of *D. persicus* eggs in a *C. gigantea* fruit is positively correlated with the fruit size.

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Distribution, development biology and behavior of *Dacus persicus* associated with *Calotropis gigantea* in Sri Lanka

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Abstract: *Calotropis gigantea* (Crown flower, Giant milkweed or Wara) is a native medicinal plant in Sri Lanka. It is recorded as an invasive plant in Australia, Brazil, USA, etc. *Dacus persicus* is recorded as a highly destructive monophagous pest of *C. gigantea* in Sri Lanka. Larvae of *D. persicus* feed on developing fruits and seeds and reduce the reproductive output of the plant significantly making it a suitable candidate for biocontrol. Therefore, the present study was aimed to investigate the distribution and reproductive biology of *Dacus persicus* to assess the potential as a biocontrol agent for *Calotropis* species. *D. persicus* distributed in six provinces in Sri Lanka. The duration of mating and ovipositing of *D. persicus* was 54 and 92 minutes, respectively. It laid eggs in the seed chamber of developing fruits and the fruit size is highly correlated ($p < 0.001$, $r = 0.990$) with the number of laid eggs. Only one egg cluster of *D. persicus* found within a single fruit having 18.5 (± 0.85) eggs per cluster and the eggs hatched in 3 days. The duration of larval and pupal stages for *D. persicus* were 24 and 12 days, respectively. These results provide essential information needed in adopting *D. persicus* as a biocontrol agent of *C. gigantea*.

Keywords**:** *Calotropis gigantea*; *Dacus persicus*; invasive species; biocontrol.

INTRODUCTION

Calotropis gigantea (Apocynaceae) (L.) W.T. Aiton. (Crown flower, Giant milkweed or Wara) is a tall plant or a shrub which grows up to 2.4 – 3 meters (Singh *et al*., 2014). It consists of well developed, branched root system and all parts of the plant consist of whitish, thick latex (Kumar *et al.,* 2013). It is native to India, China, Sri Lanka, Malaysia (Dhileepan, 2014), Bangaladesh, Pakistan, Indonesia, Camboidea, Thailand and Philippines (Islam *et al.,* 2019) and also distributed in several countries in South Asia, the Middle East, Africa and in North and South America (Kumar *et al*., 2013). It is an exotic, invasive species in Australia, Virgin Islands of United States, Mexico and Brazil (Kumar *et al*., 2013; Amutha *et al*., 2018). Plants grow well on abandoned over-cultivated area; over-grazed grounds, roadsides, lagoon edges and disturbed sandy soil (Kumar *et al*., 2013).

Calotropis species are subjected to herbivory by several insect and mite species in its native range. According to Al dhafer *et al*. (2011), in Western region of Saudi Arabia, 24 species of insects are associated with *Calotropis procera* (L.) W.T. Aiton while in Central region 99 species of insects are associated with *C. procera*. Though latex of the *C. procera* plant is considered toxic to insects (Al dhafer *et al.,* 2011), large number of insect pests cause considerable damage to the plant (Saikia *et al.,* 2015). Dhileepan (2014) recorded sixty-five insect species associate with *Calotropis* spp. in their native range. Among them, more than 50% of insects feed on leaves while others feed on flowers, stems, seeds, and fruits. Most of the insects associated with *Calotropis* species were recorded from India (Dhileepan, 2014). In contrast, there are few insect species found feeding on the *Calotropis* species in its introduced countries. Aphids, grasshoppers, and caterpillars of *Danaus* spp. are considered as common plant feeders associated with *C. procera* (Al dhafer *et al.,* 2011). *Danaus* spp. are not considered as severely damaging pests in Australia, Hawaii, Fiji, Brazil, Jamaica, and Puerto Rico (Dhileepan, 2014). Most of the insects associated with *C. procera* are polyphagous while, *Dacus persicus* Hendel (Diptera: Tephritidae) is considered as a major insect pest specific to *Calotropis* species (Dhileepan, 2014).

Dacus persicus, commonly known as Aak fruit fly, is a monophagous insect of *Calotropis* species (Dhileepan, 2014). It is native to India, Sri Lanka, Iran, Pakistan, and Iraq. The closely related species, *Dacus longistylus* Wiedemann, is also a monophagous insect associated with *Calotropis* species. It is distributed in Sudan, Egypt, Israel, Saudi Arabia, Iran, Senegal, Kenya, Nigeria, Mali, Eritrea, Libya, UAE, and Niger (Dhileepan, 2014). *D. persicus* larva is one of the destructive seed feeders of *Calotropis* species (Sharma and Amritphale, 2008). Gravid *D. persicus* females lay eggs inside developing *Calotropis* fruits by penetrating the skin of fruit with its ovipositor (Parihar, 1984). Emerging *D. persicus* larvae feed and grow within the developing fruits. Infested fruits, rot and often drop prematurely. Fully developed larvae drop from the fruits into the ground and pupate in soil (Dhileepan, 2014). The damage caused by *D. persicus* drastically influence the reproductive output of the plant there by significantly reducing the plant dispersal and population growth.

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When monophagous insect acts as a pest, normally it causes a considerable damage to the host plant. The ability to cause severe damage to their host plant, and being host specific are ideal characteristics that make the insect, the *D. persicus* as a promising weed biocontrol agent for *Calotropis* species in its introduced countries. In introduced countries, the plant is regarded as highly invasive and so far, there is no successful chemical or mechanical method to control the dispersal of the plant. Therefore, the weed biologists highly pay attention on classical biocontrol methods and focus on monophagous insects of *Calotropis gigantea* in their native range. As C. *gigantea* is a native plant in Sri Lanka and since no studies have been conducted on *D. persicus* of *C. gigantea* in Sri Lanka, the present study focuses on understanding damage caused to the host plant, distribution, mating, oviposition and life cycle of *D. persicus* in Sri Lanka with an aim to seeking the possibility of using it as a biocontrol control agent for *Calotropis* species in Australia and in other introduced countries where the plant is regarded as invasive.

MATERIALS AND METHODS

Field sampling of *Calotropis gigantea* within Sri Lanka

Field visits were conducted in 120 sites in nine provinces of Sri Lanka (Figure 1) from December 2014 to June 2015. Sampling was conducted at monthly intervals and each site was sampled only once. Roadside sampling sites were selected randomly at 30 minutes intervals while traveling on a vehicle with a speed of 50 km per hour. If a new site with *C. gigantea* was not observed after 30 minutes, traveling was continued until a site having *C. gigantea* is found. In every sampling site, occurrence data of *C. gigantea* distribution (GPS coordinates) was recorded. In every site, associated insect fauna of *C. gigantea* were observed within 30 minutes time duration. During the survey, insects associate with the plant were photographed. The insects including *D. persicus* were collected directly from various parts of the plant (leaves, flowers, flower buds, stems, and fruits) by hand-picking. 2-3 individuals of same species in each site were collected to small plastic vials for morphological identification. The specimens were deposited in the Department of Zoology laboratory, at the University of Ruhuna, Sri Lanka. Specimens were identified up to genus/species level under the guidance of Entomologists of Entomology Division, The Horticultural Crop Research and Development Institute (HORDI), .Gannoruwa, Sri Lanka

Monthly field sampling of *Calotropis gigantea* within Southern Province

To study the reproductive biology and temporal variation of *D. persicus*, eleven sites from Southern province having easy access from University of Ruhuna were selected. The sites were Kalametiya (6° 6’N; 80° 55’E), Medilla (6° 2’N; 80° 48’E), Tangalle (6° 1’N; 80° 47’E), Nalagama (6° 4’N; 80° 47’E), Dadalla (6° 2’N; 80° 11’E), Thalpe (5° 59’N; 80° 16’E), Habaraduwa (5° 59’N; 80° 18’E), Kathaluwa (5° 58’N; 80° 20’E), Kamburugamuwa (5° 56’N; 80° 29’E), Devinuwara (5° 55’N; 80° 34’E) and Palena (5° 56’N; 80° 29’E). The above sites were consisted of three sites from Matara district and four sites each from Hambantota and Galle districts, representing both coastal and inland regions. Hundred meters towards to the island from seashore was considered as coastal region while rest of the regions of the island was considered as inland regions. Monthly surveys were conducted from August 2015 to August 2016 and each site was sampled twice a month. At least six *C. gigantea* plants (maximum eight plants) approximately similar in size were selected from each site and numbered the stems of the plants with white paints. During field visits, the abundance (number of adults per plant), their activities (walking, resting on leaves and fruits) on the plant and intra-species interactions (female-female fruit flies and male-female fruit flies) of *D. persicus* on marked trees were recorded.

Life cycle studies

In parallel to field studies, *D. persicus* was reared in the laboratory to study the mating and oviposition behavior, and durations of larval and pupal development. Male and females of *D. persicus* were collected from the study sites from Southern Province (directly by hand picking and placing them into small plastic vials) and transported to University of Ruhuna. *D. persicus* adults were maintained in transparent plastic boxes covered with insect-proof wire mesh material on top. Adult *D. persicus* was fed with bee honey and sugar solution.

Mating and oviposition behavior

To study oviposition behavior of *D. persicus*, fresh *C. gigantea* fruits having developing whitish seeds (fruit length 4.2 - 10.7 cm/ fruit width 2.68 - 7.64 cm) were placed in rearing cages. The fruits that were selected for oviposition were labeled and observed whether more than one fruit fly oviposit on a single fruit. The oviposition duration of each fruit fly was recorded. Mating behavior of *D. persicus* was recorded by observing activities of pre-mating, mating and post mating under the natural in the field. Similarly, under laboratory conditions,time duration for pre-oviposition, oviposition and post-oviposition behavior of *D. persicus* were observed by the naked eye.

Extraction of eggs of *D. persicus*

Two hundred and fifty (250) *C. gigantea* fruits having whitish-developing seeds (fruit length 4 – 11 cm/ fruit width 2 cm) were collected monthly from 11 selected sites and transported to laboratory. Egg clusters of *D. persicus* were extracted from infected fruits under laboratory conditions. Before extraction, the maximum width, and the maximum length of the *C. gigantea* fruit were measured using a vernier caliper. The number of egg clusters per fruit and eggs per cluster were counted in the lab under Wild Heerbrugg stereo microscope (under the power of 15 × 40). To find any correlation between the volume of oviposited *C. gigantea* fruits and the number of laid eggs per fruit, the following equation was used.

$4/3\pi ab^2$ where,

a- Maximum length of *Calotropis* fruit / 2
b- Maximum width of *Calotropis* fruit / 2

As *D. persicus* lay eggs in immature, developing oval shaped *C. gigantea* fruits, an assumption was made as all the studied fruits were prolate ellipsoid in shape and the above equation was applied to gain the volume of *C. gigantea* fruit.

Larval development

Some of the extracted eggs, larvae, and pupae were placed back to same fruits and were reared to adults under laboratory conditions at 27 - 30 °C. In high moisture conditions, mature fruits were rotten with live larvae within the fruit. In such conditions, these larvae were transferred to seed chamber of fresh fruits and allowed them to complete larval development and facilitate pupation. The replacement of rotten fruits with fresh fruits, was done until larvae turn into pupae.

During monthly samplings, *C. gigantea* fruits oviposited by *D. persicus* (n =100) were collected randomly from field sites. They were kept under laboratory conditions and different larval stages (until final larval instar) were extracted periodically by opening *C. gigantea* fruits.

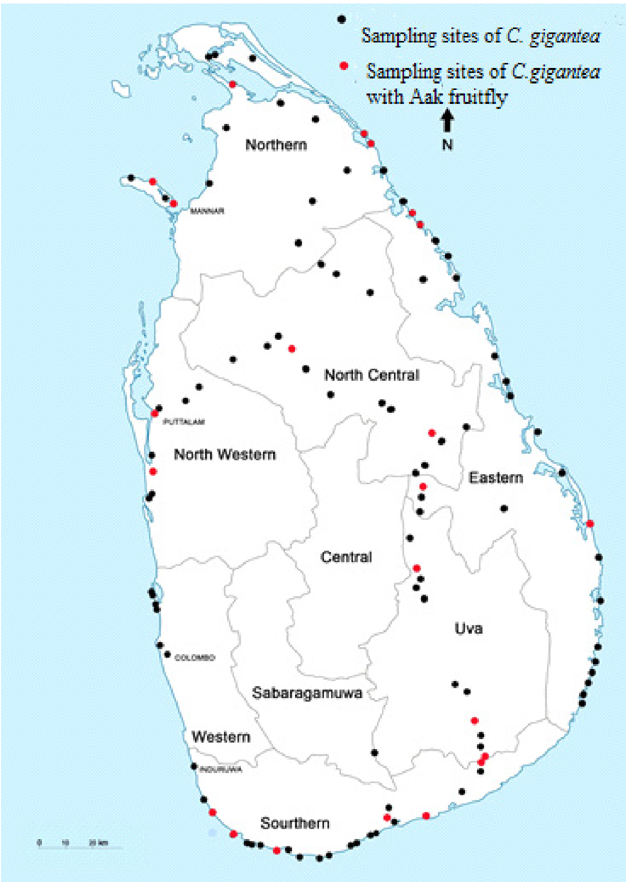

Figure 1: Sampling sites of *Calotropis gigantea* and Aak fruitfly (*D. persicus*) in Sri Lanka.

To determine the number of larval instars, larval stages were placed on 70% alcohol (Ghafoor, 2011). In order to determine the larval stage, the maximum length of the head capsule of each larva of *D. persicus* was measured using a calibrated ocular micrometer in a binocular dissecting microscope.

Data analysis

Data analysis was done using Minitab 16 Statistical software package. Mean values and standard errors related to life history data of *D. persicus* was obtained. Correlations were developed for *C. gigantea* fruit size and numbers of eggs within the fruit.

RESULTS

Distribution of *D. persicus* in Sri Lanka

D. persicus was restricted to certain districts and it was not recorded in all districts where the plant was available. *D. persicus* was recorded in the coastal as well as in the inland areas (Figure 1). However, there is no significant difference (Chi Sq - 1.63, p value - 0.201) in the presence of *D. persicus* in between coastal and inland sites. There were no records of *D. persicus* in Western province although the plant was available. There were no records of *C. gigantea* in Central Province, and therefore, *D. persicus* was absent in the Central region of Sri Lanka (Figure 1).

Temporal variation of *D. persicus* in Southern Province

D. persicus was recorded in all three districts of Southern Province. Comparatively higher abundance of *D. persicus* was recorded in Galle district while lowest abundance was recorded in Hambantota district (Figure 2). It is statistically also confirmed a difference in the mean abundances of *D. persicus* (p = 0.002) at least in two districts of Southern Province. Peak abundance of *D. persicus* was recorded during July to October while lowest abundance was observed from November to December. However no significant difference in mean abundances of *D. persicus* (p = 0.281) during study period.

Temporal variation of *D. persicus* across the sites of Galle, Matara and Hambantota

D. persicus was recorded in all sites except Kathaluwa site (Galle district) and Devinuwara (Matara district). Dadalla was the only site, where fruit flies were recorded throughout the year with high abundance (Table 1).

Life cycle studies of *D. persicus*

Mating and oviposition behavior of D. persicus

D. persicus mated any time during the day (Figure 3). They mostly paired in mornings and rarely paired in afternoons (Figure 3). Gravid females of *D. persicus* oviposit only in developing fruits with immature, milky white seeds (Table 2). Female *D. persicus* highly attracted (51.62%) for immature fruits having 1-20 cm^3 volume. Interestingly, their preference for selection of a fruit for oviposition reduces

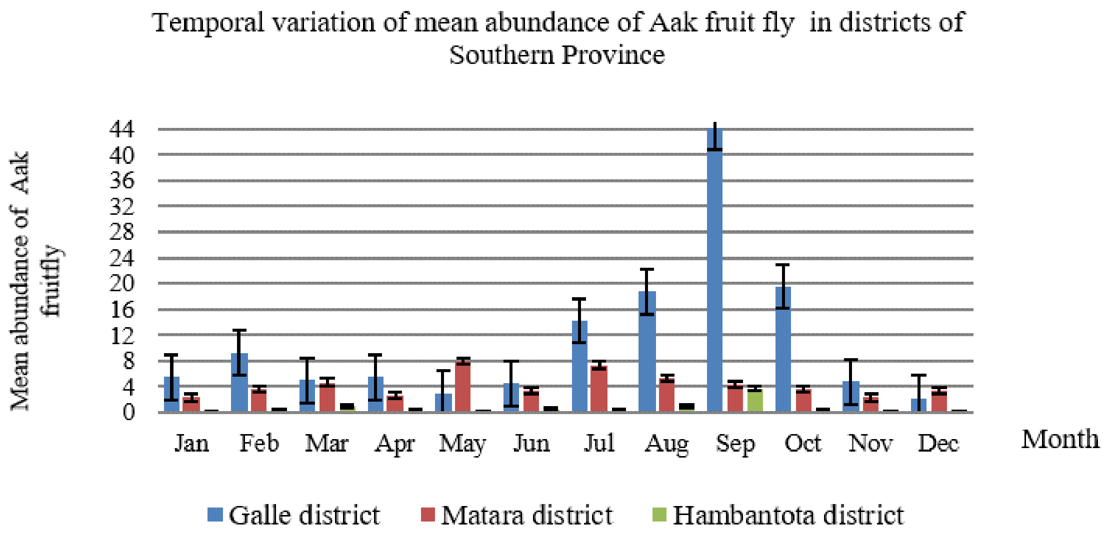

Figure 2: Temporal variation of mean abundance of Aak fruit fly (*Dacus persicus*) in districts of Southern Province.

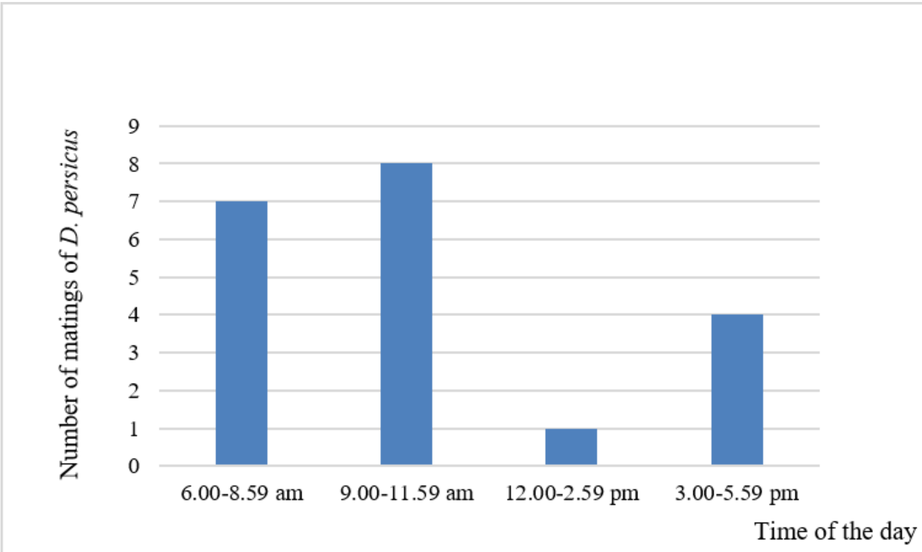

Figure 3: Number of mating of *D. persicus* with respect to time of the day.

Table 1: Temporal variation of mean abundance (± S.D.) of *D. persicus* across the sites of Galle, Matara and Hambantota districts.

District	Site	Mean abundance of *D. persicus*
Matara	Devinuwara	0.00 ± 0.00
	Kamburugamuwa	0.86 ± 1.31
	Palena	0.85 ± 1.76
Hambantota	Kalametiya	0.02 ± 0.13
	Medilla	0.23 ± 1.00
	Nalagama	0.02 ± 0.19
	Tangalle	0.10 ± 0.49
Galle	Thalpe	1.40 ± 4.49
	Habaraduwa	0.16 ± 0.66
	Kathaluwa	0.00 ± 0.00
	Dadalla	6.06 ± 8.48

into half when fruit size is doubled (Table 2). Statistically also proved that there is a strong correlation (r = -0.933, p = 0.020) between the volume of fruit and fruit selection for oviposition by *D. persicus*. Similarly, when volume of the fruit increases the amount of laid eggs laid also increase (Table 2) indicating a strong correlation (r = 0.968, p = 0.007) between the number of eggs of *D. persicus* within the *Calotropis* fruit.

D. persicus place eggs inside the seed chamber of *C. gigantea* fruit by directly piercing the fruit by its ovipositor (Figure 4). Field observations revealed, there was a great competition for selection of fruits for oviposition. Few females (4 - 5 individuals) showed walking on such fruits and aggressive behavior (chasing fruit flies away from the fruit) among female fruit flies were observed. In such conditions, 2 - 3 females of *D. persicus* oviposited in the same fruit. Even though, a female fruit fly was already in the oviposition, process, other (one or two) fruit fly females start their oviposition within the same fruit. The latter ones also expend approximately same time for the oviposition process, as initially oviposited fruit fly. Even though multiple oviposition of *D. persicus* females on the same fruit was seen; only one egg cluster per fruit was recorded. Personal experience revealed that, the prevailing egg cluster was closer to the oviposition punch of the initial female fruit fly.

Eggs, larvae and pupae of D. persicus

The eggs of *D. persicus* were pale whitish, delicate, elongate, slightly curved, tapering towards either side and arranged similar to a bunch of bananas (Figure 4). After 2.87 (± 0.62) days of oviposition, the first instar larvae of *D. persicus* was emerged. The developing larvae were creamy white in colour with brownish head capsule with mandibles and prolegs. *D. persicus* consisted of three larval instars. Survival of eggs was recorded as 64.38%.

The pupa of *D. persicus* was cylindrical in shape but rounded at both ends and dull creamy white in color with horizontal rings like ridges (Figure 4). *D. persicus* emerged from pupa at daytime was pale brownish in color (Figure 4). Under laboratory conditions, about 59% of larvae reached pupal stage, and about 50% pupae emerged as adults. In laboratory conditions, newly emerged individuals represented the sex ratio as 1:1. In the field studies, it was recorded as female abundance was higher than males.

Damage levels of D. persicus

Larval development of *D. persicus* took place within the *Calotropis* fruit. With respect to larvae of Aak weevil (*P. farinosa*) (Wijeweera *et al*., 2020), *D. persicus* larvae voraciously fed on developing seeds of *C. gigantea* fruit causing severe damage to seeds. The present study revealed that all larval stages feed on seeds and destroy (100% of the seeds) the infected fruit. When it was about to pupate, larvae consume all the seeds of infected fruit. During this stage inner seed chamber appear as a decaying sponge and such kind of fruits can be easily identified through its external features such as pale yellowish, malnourished and stunted nature. However, adult *D. persicus* were harmless to *C. gigantea* as they feed on naturally occurring sugary compounds and under laboratory condition, they feed on artificial sugar solutions.

DISCUSSION

There is a close association between *D. persicus* and its host plant as it provides shelter, food, oviposition sites and mating grounds (Aluja and Liedo, 2013). When considering monophagous pests, they only survive if the host plant is available. Similarly, in this study also, the distribution of *D. persicus* is closely associated with its host plant *C. gigantea* (Figure 1). Dadalla was the only site where *D. persicus* appeared throughout the year. It may be due to resource availability around the sampling area. *D. persicus* was recorded in all sites of Hambantota district. It may be due to climate suitability of the district for survival of *D. persicus*.

Life history studies reveal that *D. persicus* oviposit on developing fruits. This may be due to two major reasons. Developing fruits are easy to penetrate and ensure the placement of eggs in the inner seed chamber and the middle fibrous layer. On the other hand, developing fruits having immature seeds; a suitable food source for newly

Table 2: *Calotropis* fruit size categories, maturity status of *Calotropis* fruit, percentage fruit selection for oviposition according to fruit volume and mean number of *D. persicus* eggs within the C*alotropi*s fruit according to fruit volume.

***Calotropis* fruit size according to the volume**	**Maturity of *Calotropis* fruit**	**Percentage fruit selection for oviposition according to fruit volume**	**Mean number of *D. persicus* eggs within the *Calotropis* fruit according to fruit volume**
1-20 cm^3 (Category 1)	Immature	51.61	13.13 ± 5.49
21-40 cm^3 (Category 2)	Immature	25.81	17.00 ± 6.61
41-60 cm^3 (Category 3)	Immature	12.90	17.50 ± 2.89
61-80 cm^3 (Category 4)	Immature	6.25	19.50 ± 3.54
81-100 cm^3 (Category 5)	Immature	3.22	21.00 ± 0.00
101-120 cm^3 (Category 6)	Mature	0	0
121 cm^3-above (Category 7)	Mature	0	0

Table 3: Life history data, field incident data and reproductive data of *D. persicus.*

Index	**Average (Number ± S.E) / Percentage**
Mating time period (in minutes)	53.80 ±1.68 (n-20)
Duration of oviposition (in minutes)	92.31 ± 2.62 (n-13)
Duration of post oviposition (in minutes)	18.75 ± 2.98 (n-8)
Incubation period (in days)	2.87 ± 0.62 (n-31)
Duration of larval development (in days)	24.19 ± 0.47 (n-37)
Duration of pupal development(in days)	11.72 ± 0.26 (n-18)
Number of eggs per egg cluster	18.5 ± 0.847 (n-31)
Number of larvae per infested fruit	11.91 ± 1.27 (n-44)
Number of pupae produced from infested fruit	7.04 ± 1.13 (n-22)
Number of newly merged adults per infested fruit	3.52 ± 0.772 (n-22)
Head capsule width of first larval instar (mm)	0.30 ± 0.04 (n-18)
Head capsule width of second larval instar (mm)	0.47 ± 0.07 (n-191)
Head capsule width of third larval instar (mm)	0.78 ± 0.11 (n-138)
Length of egg (mm)	1.35 ± 0.001 (n-66)
Length of a pupae (mm)	0.65 ± 0.006 (n-60)
Width of a pupae (in mm)	0.29 ± 0.004 (n-60)

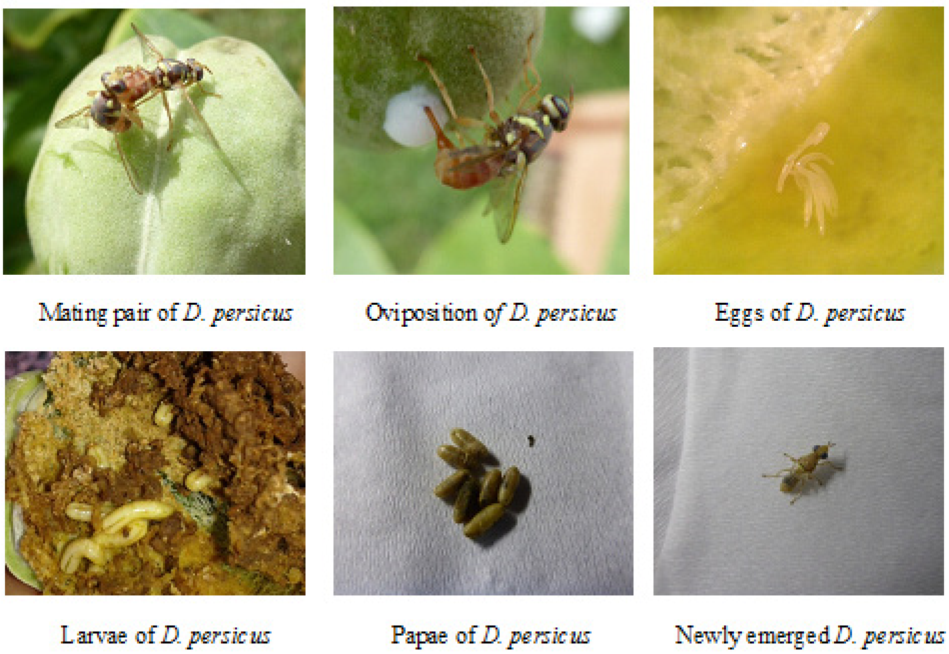

Figure 4: Life cycle stages of *Dacus persicus*.

emerged larvae with delicate, developing mouthparts. It is recorded that female gravid *D. persicus* are more attracted to soft fruit morph than hard fruit morph of *C. gigantea* due to the high penetrability of the ovipositor into soft morph fruits than hard morph (Sharma and Amriphale, 2007). Male *D. persicus* associates with developing fruits, during the oviposition period of females. It may be due to easy accessibility to females for the mating process and territory marking on suitable host fruits for facilitating females for oviposition (Aluja and Liedo, 2013). Pre- and post-oviposition behaviors of *D. persicus* are very similar to those observed in *D. longistylus* (Parihar, 1984).

Dissected fruits reveal that *D. persicus* eggs are in the inner seed chamber of the fruit or sometimes among seeds. The newly emerged fruit fly larvae contain weaker mandibles which are not strong enough to penetrate the inner pericarp layer of the fruit. To avoid the barrier, female *D. persicus* penetrate the inner pericarp layer by their long ovipositors and ensure the eggs are placed in the seed chamber. Although 2 - 3 *D. persicus* females oviposit on a single fruit, dissected fruits contain only one egg cluster per fruit. It may be due to pseudo- oviposition of female fruit flies. Similarly, several females of *Toxotrypana curvicauda* Gerstaecker (a fruit fly), oviposit on single fruit but no multiple clusters of eggs in the fruit (Aluja and Norrbom, 1999). In addition, studies of Tephritid fruit flies reveal that they mark the oviposited fruit using host marking pheromones. It signals the other female fruitflies that the fruit is already used for an oviposition (Scolari *et al.,* 2021). It may a possible reason of having only one cluster of eggs per *Calotropis* fruit. The eggs of *D. persicus* are longer (1.35 mm) than *D. longistylus* (1.00 mm) eggs (Parihar, 1984). Similarly, the pupae of *D. persicus* (0.65 mm - length, 0.29 mm – width) are larger than *D. longistylus* (0.45 mm - length, 0.2 mm width) pupae (Parihar, 1984).

The third larval instar of *D. persicus* pupates in soil by forming burrows at 3 - 5 cm deep (Sharma and Amriphale, 2008). Newly emerged *D. persicus* adults are lighter in color and unable to fly. However, within 15 minutes of emergence, they were able to fly.

D. persicus reared in the laboratory had a 1:1 sex ratio of female and male. In field observations, the female fruit fly abundance was higher than males. Normally female fruit flies have to choose a proper mate, mate with the selected partner, bear their eggs until maturation, find a suitable fruit to oviposit and lay their eggs. For a male fruit fly, their reproduction role is limited only to find a mate by competing with other male fruit flies and mating. Contribution of female fruit fly to generate new progeny is comparatively higher than male flies. For the effectiveness of the process, female fruit flies should live longer life. The observation of higher abundance in female fruit flies than male may occur due to the long lifespan of female fruit flies.

CONCLUSIONS

The findings of the present study provide detailed information on distribution, intensity of damage to the host plant, mating, oviposition and life cycle stages of *D. persicus* in Sri Lanka where no known records are previously available. As *D. persicus* feed on all the seeds (100%) of infected *Calotropis* fruit, it greatly influences on reproductive output and ultimately dispersal of the plant. Therefore, the present study will provide essential information for further studies of *D. persicus* in *Calotropis* spp. to seek the possibility of using it as a biocontrol agent.

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DECLARATION OF CONFLICT OF INTEREST

The authors have no conflict of interest or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in the manuscript.

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