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ORIGINAL ARTICLE

Pollinators of *Ecbolium ligustrinum* (Vahl) Vollesen: A Shifting from Melittophily to Myophily

Arijit Kundu, Pankaj. K. Pal[1] and Prakash Karmakar*
Palynology and Plant Reproductive Biology Section, Department of Botany and Forestry, Vidyasagar University, Midnapore, West Bengal, India-721102
[1] Palaeobotany and Palynology Section, Department of Botany, Centre for Advanced Study, The University of Burdwan, Golapbag, Burdwan, West Bengal, India-713104
***Corresponding author**: **E-mail:** karmakar_p@yahoo.co.in

ABSTRACT
While studying the reproductive ecology of Ecbolium ligustrinum (Vahl) Vollesen, a member of Acanthaceae with special emphasis on floral visitors vis-à-vis pollinators, it has been found that 8 species of insects visit the plant during its flowering period. Investigations regarding foraging behaviour of the visitors entail a difference between efficient pollinators, nectar robbers, pollen thieves and less efficient pollinators. The principal pollinator is Eristalis sp. a dipteran fly of Syrphidae. Other less efficient pollinators are the three ant species of Hymenoptera. The remaining visitor members belong to the order of Coleoptera, Hemiptera, Hymenoptera and Lepidoptera. The plant shows a complex floral morphology, with apparently bee-pollinated syndrome. However, the plant offers nectar and mainly pollinated by a fly species through the dorsal surface of the insect (nototribic). Specific ecological niche with complex floral morphology may furnish a selective pressure that leads the shifting of typical melittophily to syrphid myophily displayed by the flower of E. ligustrinum.
Keywords: *Ants, Ecbolium ligustrinum, Eristalis, Floral visitor, Pollinator.*

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INTRODUCTION

Pollination is a key mutualism between two kingdoms of organisms, in which plants offer a reward to flower visitors that transport pollen among conspecific plants resulting in plant reproduction [1, 2, 3, 4]. Around 90% of all flowering plants are animal pollinated [5, 6, 7]. Animals, particularly insects, play an important role in pollen transfer during pollination. During evolution of flowers particularly for specialization, role of animal visitors is important and depend on their pollination effectiveness where reproductive success is pollen-limited [8, 9]. Pollination effectiveness refers to the input supplied by animal visitors to plant's fitness through pollination [10, 11, 12]. This contribution of fitness can be measured in terms of the animal's pollination efficiency and its visitation frequency on flowers [10, 11, 13, 14]. Correlations between certain floral characteristics of plant species and kind of animal pollen vectors that visit their flowers are well known. In many cases, a parallel evolution between plants and their pollinators has been established [15]. However, for some plant species, the most frequent animal visitor cannot be predicted by floral morphological characters [16, 17, 18, 19]. For example, flowers of different species of cacti in the Sonoran desert exhibit apparent bat pollination syndrome, however, seed setting of those species is done by birds [18]. Similarly, flowers of *Ipomopsis aggregata* are pollinated by long-tongued bumblebee *Bombus oppositus* despite the flowers' apparent hummingbird syndrome [20].
Ecbolium ligustrinum (Vahl) Vollesen also known as green shrimp plant belongs to the member of Acanthaceae is a perennial woody herb and native to India and Sri-Lanka. Besides, the plant is also found in Arabian Peninsula, Somalia and countries of tropical Asia. The plant mainly grows in shady places as an understorey of trees forming clumps in isolated patches. Inflorescence in dense terminal spikes ranges 5.2-14.2cm. Flowers are nearly sessile, 4.9-5.9cm in length having one large leafy green bract and 2 small

scaly bracteoles. Flowers zygomorphic, connate in a 2- lipped corolla (bilabiate), forming long tube of 3.2-3.5 cm, almost filiform; posterior (upper) lip linear, hoodlike in early phase, later reflexed like the long antenna of a shrimp and shortly bi-fid; anterior (lower) 3-lobed spreading having a landing space for a visitor; middle lobe with a ladder like groove and furrow for an easy approach of a visitor towards mouth of the bilabiate corolla for nectar. Flowers greenish during early phase of the day and turn blue for the later half up to senescence. Male reproductive apparatus consists of two epipetalous stamens fused with the upper lip of the corolla just exposing the anthers downwardly in an open flower. Carpel connate in a 2-celled ovary; style-1, slender, terminal; exerted with soft transmitting tissue, 38-42 mm long, somewhat flexible in nature. The distal part of the style beyond the corolla tube is about 6-9 mm long running through the middle of the two anthers along the ventral surface. Stigma slightly bifid, dry with papillate receptive surface. The whole gynoecium is persistent with marcescent type, after senescence of corolla the style remain in a hyperbolic configuration up to 2 days and then started to shrivel.

Flowers of *Ecbolium ligustrinum* shows a complex floral morphology closely conform to bee pollination syndrome. However, the plant is primarily pollinated by *Eristalis*, a dipteran fly and to a lesser extent by three taxa of hymenopteran ants' viz. *Camponotus*, *Formica* and *Monomorium*. Myrmecophily i.e. ant-plant interaction that leads to pollination is rare indeed in plant system.

As the plant exhibits a floral morphology symptomatic of marked entomophily and solely dependence of insects for pollination, the objective of the work is to study the insect pollen visitors, their frequencies, their behaviour on the flower and the degree of specialization regarding floral morphology for a better suitability of pollination and seed set.

MATERIALS AND METHODS

The floral visitors were surveyed on ±275 flowers/year of *Ecbolium ligustrinum* during June to December for 2013, 2014 and 2015 in Chandannagar of Hoogly Distict of West Bengal, India. River Ganges flows its lower course through the area and thus, climate is of tropical humid type having dense vegetation. Representative samples were captured at different times of the day using an entomological net, immobilized with ethyl acetate soaked cotton in borosil glass vials and dried with silica gel. Taxonomic identification of the visitors was done with the help of entomologists, Zoological Survey of India, Ministry of Environment and Forestry, Govt. of India and from the available literature [21]. The activity of the visitors in and around an individual flower was observed minutely starting from flower opening to senescence with unaided eyes and also by using a 10x hand lens. The visitors were carefully studied under a Leica WILD M3B Stereo-binocular microscope to detect the presence of pollen (if any) on their body parts and mode of pollen deposition. Bagging experiments were also performed to ascertain whether any pollen deposition over stigma could occur in absence of the visitors. Flowers were bagged with appropriate nylon net restricting the visitors' activity and allowing the free-flow of wind-borne pollen grains (if any). The stigmas of such flowers were examined at the end of the day with a Leica WILD M3B Stereo-binocular microscope to detect the presence of any deposition of pollen. Some bagged flowers were also kept under day-to-day observation to determine whether any fruit-set occurred in such flowers or not.

Among the visitors, potential pollinators were identified by judging the following pollination postulates:

1. Coincidence of the visitation with the duration of anthesis (pistillate and staminate floral phase).
2. While visiting a flower, chance of the visitor to come in contact with the reproductive organs i.e. the dehisced anthers and receptive stigma.
3. Adherence of pollen grains to the body surface of the visitor.
4. Interfloral movement of the visitors [22].
5. Role of the visitor in pollen deposition over stigma in controlled pollination experiment.

After ascertaining the pollinators from the rest of the floral visitors, the pollination efficiency of the pollinators were determined. For this, shoots with several target flower buds of different experimental plants were bagged individually with a fine mesh and the buds were tagged properly. The bags were large enough allowing the flowers to open completely without any disturbances inside the net. After complete opening of individual virgin flower for each plant, only single visitor was allowed to visit by preventing the entry of other visitors through experimental set-up. Observations were carried throughout the day and numbers of visits were recorded up to the cessation of stigma receptivity. Fruit development was recorded after visited by individual visitor and fruit-set percentage was calculated. Such experiment was performed in every month during the flowering season.

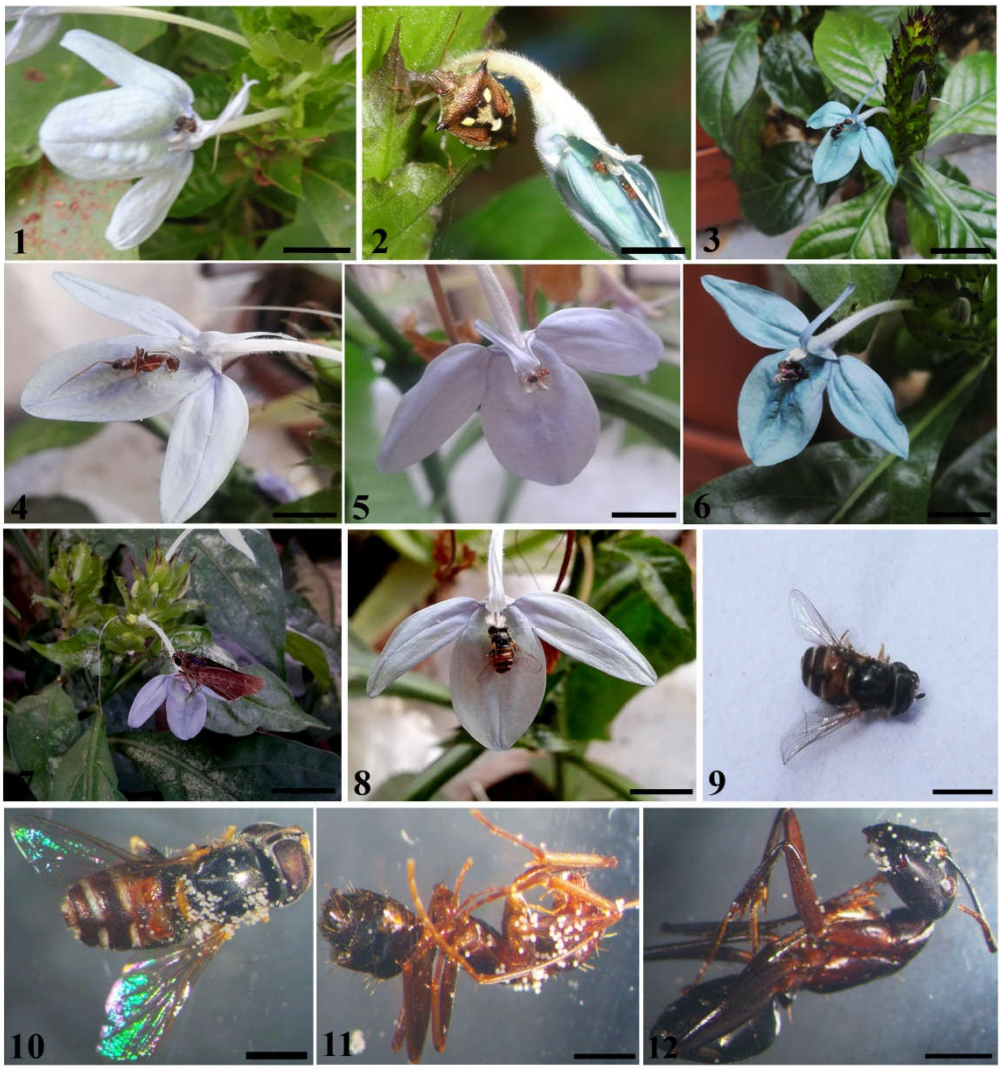
RESULT AND DISCUSSION

Categorization of flower visitors:

The flowers of *Ecbolium ligustrinum* have been found to visit by 8 species of insects in total. The visitation pattern and activity of the visitors are presented in detail in Table 1.

Floral visitor of *E. ligustrinum* can be classified into the following three categories on the bases of the activities performed by them.

PLATE - 1



1. *Cryptocephalus* 2. *Acanthosoma* 3. *Camponotus* 4. *Formica* 5. *Monomorium* 6. *Cymus* 7. *Pseudoborbo bevani* 8. *Eristalis* visiting the flower 9. An elaborate form of *Eristalis* 10. Nototribic adherence of pollen grains on *Eristalis.* 11. Pollen grains attached to the legs and ventral surface of the body parts of *Formica* 12. Pollen grains adhered to the head and mouth parts of *Camponotus* Scale bar - 0.5 cm.

Category-I: A small fly of the genus *Eristalis* (Plate.1, fig.8, 9, 10) and three different species of ants belonging to the genera *Camponotus* (Plate.1, fig.3, 12), *Formica* (Plate.1, fig.4, 11) and *Monomorium* (Plate.1, fig.5) respectively are considered under this category. Individual members of this category are found to dominate the visitors' population of *E. ligustrinum* by visiting the flower most regularly throughout the flowering season. The *Eristalis* sp. visit the flower since early morning (7.30-8.30 am) up to the late afternoon (4.30-5.30 pm) and are seen to feed the nectar stored within the corolla tube entering by the throat of the corolla tube. The visitation frequency of the fly species gradually increases

with the progress of time up to 3.00-3.30 pm and then declines rapidly during afternoon. Maximum activity of this fly is noticed during 11.00-3.00 pm throughout the entire flowering season. The configuration of the two anthers as well as stigma is so adjusted that during nectar foraging the pollen grains from the dehisced anthers were smeared on the dorsal surface of the fly and concomitantly encountered with the receptive stigma, thus pollinate the flower nototribically.

The three hymenopteran members of ant viz. *Camponotus*, *Formica* and *Monomorium* show more or less similar pattern of activity and visitation frequency throughout the day. They started their visitation at about 5.00-600 am in the morning and continued up to 6.00-6.30 pm in the evening. *Camponotus* and *Formica* exhibit their maximum frequency during 8.00 am to 4.00 pm while *Monomorium* shows its highest occurrence during 9.00 am to 4.00 pm. In an open flower stage they were seen to visit for both pollen grains and nectar. All the ant species collect nectar from the corolla tube as well as from the extrafloral nectarines situated at the base of the calyx as glandular hairs. In fact, the ants visit here and there searching nectar all through the flower and during visitation pollen grains are adhered to their heads, legs, tentacles and ventral surfaces of their bodies. In this way they also visit and stay over the dry stigma unknowingly and pollinate the flower sternotribically. Here, the ants mainly perform the autogamous type of pollination and sometimes geitonogamy.

By considering the activities of the above mentioned visitors it may be concluded that *Eristalis*, is the most effective pollinators and *Camponotus*, *Formica* and *Monomorium* are the less effective pollinators of *Ecbolium ligustrinum* which is again confirmed by the following observations:

1. The duration of anthesis coincides with their time of visitation.
2. It has been observed that during their visit on a flower, they get in touch with the dehisced anthers and stigmatic lobes.
3. Clump/dispersed pollen grains have been found to adhere on the body surface of the pollinators, here pollens are found on the dorsal surface of *Eristalis* and ventral surfaces of the ants (Plate-1, fig.10, 11, 12).
4. No pollen grains were found to deposit on the stigmatic surface in bagged flower i.e. without any visitor.

Category-II: A coleopteran member, *Cryptocephalus* sp. (Plate.1, fig.1) belongs to this category. Here, the insect is a moderate to rare visitor of the *E*. *ligustrinum. Cryptocephalus* visits the flower from late morning (10.00-11.30 am) to early afternoon (3.30-4.00 pm) and are seen to feed on the dehisced anthers. After getting pollen, they scroll through the petal lobes and then move to another flower. But they did not explore the stigma during their visit. Therefore, the said visitor of this category cannot be considered as pollinator; rather they may be regarded as pollen thieves.

Category-III: The two Hemipteran members' viz. *Acanthosoma* (Plate.1, fig.2), *Cymus* (Plate.1, fig.6) and a Lepidopteran species the *Pseudoborbo bevani* (Plate.1, fig.7) belong to this category. *Acanthosoma* moderately visit the flower from early morning (6.00-8.30 am) to noon (11.30 am-12.00 pm). They are seen to feed on the exudates secreted from the glandular hairs present over the corolla tube and calyx at the flower base quietly for 1-5 mins and after getting such secretory substances move to another flower of the same inflorescence and then to another inflorescence. The other two members of this category, *Cymus* sp. and *Pseudoborbo bevani* (Bevan's swift) visit the flower in moderate to rare instances and they have been found to explore the secretary products stored within the corolla tube for 4-6s per visit and then fly away for another one. The above said members of this category never encountered the reproductive organs of the flower. Therefore, the aforesaid visitors of category-III are purely nectar foragers and perform no role in pollination. They are mere nectar robbers of the plant species.

A detail observation regarding the performance of all the visitors of *E*. *ligustrinum* demonstrate that the species of *Eristalis, Camponotus, Formica,* and *Monomorium* are the successful pollinators of the plant. Thereby, the plant is oligophilic in nature, at least in this part of the country.

Activity of pollinators in a flower, mode of pollen presentation and the pollen transfer mechanisms:

As discussed earlier, four insect species viz. *Eristalis*, *Camponotus*, *Formica* and *Monomorium* are the pollinators of *E*. *ligustrinum*. They dominate over the other visitors of the plant by their frequency, regularity and duration of visit.

The visitation rate and time duration of *Eristalis* sp. in *E*. ligustrinum during different months of the flowering season are presented in Table 2.

Individuals of *Eristalis* sp. visit the flower frequently from 11.00 am - 3.00 pm on the day of flowering. The stamens in the early morning of freshly opened flower situated in tightly adpressed conditioned to the upper lip of the flower and stigma pointed distally little far from the anther lobes by laying the slender style through the upper surface in the middle of the anther lobes. During 11.00-11.30 am due to forward bending of style and corolla tube the gap between anthers and mid-petal lobe of lower lip also decreases.

In such floral architectural condition the pollinator species hovers around the opened flower and lands momentarily on the mid-petal lobe of the lower lip. Then the fly slowly moved through the stair like folding towards the mouth of the corolla tube to feed the nectar stored within it. During this phenomenon dorsal surface of the head and thorax of the insect encountered with the exposed anthers and profuse powdery pollen mass adhered to its body. After performing such activity it leaves the flower and again acts the same on another one. Hence, the means of pollen deposition is imprecise here i.e. 'mesh and soil' type [23], and transported nototribically (by the upper side of the body of the pollinator).

After adhering the pollen mass by the pollinator, when lands on another flower to collect nectar, the body size of the fly and the gap between stigma and petals of lower lip is so adjusted that while travelling towards nectar the dorsal surface of the body of the pollinator encountered the stigma atleast twice for a to and from movement. Therefore, the spathulate receptive stigma lobes get pollinated nototribically with the adhering pollen masses. Thus, the pollen presentation of *Eristalis* sp in *Ecbolium ligustrinum* is ensured by offering the edible nectar as reward, which also facilitates the pollen transfer to the rewardless stigma. The specific phenological events and arrangements of different floral parts are the key machinery to do so.

In addition to *Eristalis*, other three representative pollinators are *Camponotus*, *Formica* and *Monomorium*. As ants are mainly nectar foragers, therefore their visitation restricted only up to the mouth of the corolla tube and sometimes at the bases of the corolla tube. The role of ants as negative performer on male function has been established. In tropical and temperate countries ants secrete chemicals which inhibit pollen hydration and germination [24, 25, 26]. It was also reported by Galen [27] that during foraging, ants displaces pistils and significantly reduces seed production. In the present investigation we observed that ants forage over both anthers and stigma during the phase of anthesis and therefore, help in pollination. Controlled experiment also corroborates our observation (Table-6). Whether the activities of ants have any impact or not on plant's reproduction has not yet been studied here. Only thing is that the ants performed a role in pollination of the plant species which is either autogamous or geitonogamous type.

The rates of visitation of these ants in *E. ligustrinum* during different months of the flowering season are presented in Table-3, 4 and 5.

Table 1: Floral visitors of *Ecbolium ligustrinum* with their time and duration of visit, frequency of visit and foraging activity in the flowers during flowering season

No. of visitors	Order family	Name of the species	Duration of visit	Peak visitation	Incidence	Activity in the flowers
1.	Diptera Syrphidae	*Eristalis* sp.	7.30am-5.30pm	11.00am-3.00pm	Frequent	Forage nectar for 4-12s in a single visit, come in contact with anthers and stigma.
2.	Coleoptera Chrysomelidae	*Cryptocephalus* sp.	11.00am-4.00pm	12.00-2.00 pm	Moderate	Feeding the dehisced anthers.
3.	Hepimtera Acanthosomatidae	*Acanthosoma* sp.	6.00 am-12.00 pm	8.00am-2.00pm	Moderate	Feeds over secreted sugary exudates present on the glandular hairs of the corolla base and calyx.
4.	Hymenoptera Formicidae	*Camponotus* sp.	5.00 am-6.30 pm	8.00am-4.00pm	Frequent	Feeds pollen grains in the dehisced anthers, glandular hairs situated outside of the corolla tube and also glands of the calyx, explores stigma.
5.	Hymenoptera Formicidae	*Formica* sp.	5.00 am-6.30 pm	8.00 am-4.00 pm	Frequent	Feeds pollen grains in the dehisced anthers, glandular hairs situated outside of the corolla tube and also glands of the calyx, explores stigma.
6.	Hymenoptera Formicidae	*Monomorium* sp.	6.30 am-6.00 pm	9.00 am-4.00 pm	Frequent	Feeds pollen grains in the dehisced anthers, glandular hairs situated outside of the corolla tube and also glands of the calyx, explores stigma.
7.	Hymenoptera Lygaeidae	*Cymus* sp.	9.30 am-4.00 pm	11.00 am-2.00 pm	Moderate	Explores nectar within the corolla tube as well as from the glandular hairs of corolla situated outside.
8.	Lepidoptera Hesperiidae	*Pseudoborbo bevani*	10.30 am-3.00 pm	12.00-2.00 pm	Rare	Searching nectar through the corolla tube.

Table 2: The rate of visitation of *Eristalis* in *Ecbolium ligustrinum,* during the entire flowering season for three consecutive years

DIURNAL FLOWERING SEASON	7.30-9.30 am.	9.30-11.30 am.	11.30-1.30 pm.	1.30-3.30 pm.	3.30-5.30 pm.
June	2.66	3.33	5.66	8.33	1.66
July	2.33	3.66	6.33	8.66	2.66
August	2.00	3.66	6.66	9.66	3.33
September	1.66	4.33	7.66	10.66	3.66
October	1.33	4.66	7.33	9.66	3.00
November	0.66	4.33	7.00	10.33	1.33
December	0.66	4.00	6.33	9.33	1.33
Mean	1.62	3.99	6.71	9.51	2.42

Table 3: The rate of visitation of *Camponotus* sp in *E. ligustrinum* during the entire flowering season for three consecutive years

Diurnal Flowering season	5.00-7.00 am	7.00-9.00 am	9.00-11.00 am	11.00 am-1.00 pm	1.00-3.00 pm	3.00-5.00 pm	5.00-7.00 pm
June	11.33	12.66	14.33	19.33	17.66	6.33	3.66
July	10.66	13.33	13.66	19.66	16.66	6.66	4.00
August	8.33	14.66	15.00	20.33	17.33	7.33	4.66
September	7.66	15.33	15.66	21.00	20.66	9.66	6.33
October	5.33	11.33	16.33	21.33	19.33	8.33	4.66
November	1.33	10.66	16.66	22.66	18.66	6.66	2.33
December	0.66	9.33	18.33	20.00	16.33	6.33	12.00
Mean	6.47	12.48	15.71	20.61	18.09	7.32	3.94

Table 4: The rate of visitation of *Formica* sp in *E. ligustrinum* during the flowering season for three consecutive years

Diurnal Flowering season	5.00-7.00 am	7.00-9.00 am	9.00-11.00 am	11.00 am-1.00 pm	1.00-3.00 pm	3.00-5.00 pm	5.00-7.00 pm
June	10.66	12.33	13.00	15.66	14.33	5.66	3.33
July	9.33	12.66	13.33	16.33	15.00	6.33	3.66
August	7.66	14.33	15.66	17.66	16.33	7.66	4.33
September	7.00	14.66	16.33	18.33	17.66	9.33	6.00
October	4.33	11.66	13.66	15.00	14.33	7.33	3.66
November	1.0	9.66	11.66	16.66	12.33	6.66	1.66
December	0.66	9.33	11.00	17.33	15.66	6.33	1.33
Mean	5.80	12.09	13.52	16.71	15.09	7.04	3.42

Table 5: The rate of visitation of *Monomorium* sp in *E. ligustrinum* during the flowering season for three consecutive years

Diurnal Flowering season	5.00-7.00 am	7.00-9.00 am	9.00-11.00 am	11.00am- 1.00 pm	1.00-3.00 pm	3.00-5.00 pm	5.00-7.00 pm
June	1.33	9.66	10.33	12.66	11.33	3.33	2.66
July	0.66	10.00	10.66	13.33	11.66	4.66	3.33
August	00	10.33	11.33	14.66	12.33	5.33	3.66
September	00	10.66	12.33	15.66	13.33	5.66	2.33
October	00	9.33	10.66	12.66	10.66	4.00	0.66
November	00	6.33	11.66	13.00	11.33	3.66	00
December	00	4.66	12.33	14.33	12.66	2.33	00
Mean	0.99	8.71	11.32	13.75	11.90	4.13	1.80

Table 6: Efficiency of different pollinators on *E. ligustrinum* observed on the basis of fruit-set percentage

Pollinators	Percentage of fruit-set (%)							
	Time of months							
	June	July	August	September	October	November	December	Mean
Eristalis sp	40.90	41.66	45.45	48.14	52.00	42.85	42.30	44.75
Camponotus sp	7.69	8.82	8.33	9.09	9.37	8.00	7.14	8.34
Formica sp	4.16	4.00	4.76	5.71	5.88	5.55	5.00	5.01
Monomorium sp	3.57	3.84	4.00	4.16	4.25	3.33	3.70	3.83

CONCLUSION

Altogather 8 species of insects visit the flowers of *Ecbolium ligustrium* for getting rewards either as pollen grains and/or nectar. Amongst those, *Eristalis*, a fly of the order Diptera and three ant species viz. *Camponotus*, *Formica* and *Monomorium* of Hymenoptera are the successful pollinators of the plant species. Regarding the pollination efficiency of the visitors (Table 6), *Eristalis* is the most effective pollinator rather than three ant taxa; although rate of diurnal flower visitation by *Eristalis* is less than ant species both in terms of time duration and frequency.

The members of Acanthaceae possess usually bilabiate gullate flowers [4] and sometimes radiosymmetric funnel/tube flowers with exserted reproductive parts (*Barleria* type). The flowers having bilabiate corolla with sex organs resided to the upper side of the pollination unit are mostly pollinated either by bees or by wasps through their dorsal surfaces (nototribic) whilest funnel/tube flowers are also pollinated by bees by their ventral surfaces (sternotribic). Likewise, the natural orientation of *Ecbolium* flower is so structured that it should be expressed as bee pollinated syndrome. However, the plant species is mainly pollinated by Dipteran fly *Eristalis*. *E*. *ligustrinum* usually a shade loving plant which grows as an understorey of tropical canopy forming plant taxa and sometimes grown on muddy roadside under shade trees. The plant flowers during monsoon and post monsoon period (June-December) when other bee attracting flowering herbs grown as an understorey are rather rare. Such a moist condition with sporadic vegetation where other myophilous especially sapromyophilus flowers grow (Asclepiadaceae, Aristolochia, Sterculiaceae, Araceae, Burmanniaceae) is a natural harbour of different types of flies viz. carrion flies, hoverflies. In such a habitat, where incidence of bees is very less, flies have taken the opportunity to pollinate a number of blossoms typically considered as melittophilous [28]. Here also, *Eristalis* sp., a hoverfly, also known as the drone fly visit the flower and pollinate it through their dorsal surface where pollen grains were adhered. This fly sp. is a common visitor to flowers, especially during late summer, monsoon and autumn and act as a significant pollinator. Adults of this hover fly are commonly mistaken for the bees that they resemble (mimic) in appearance and behavior [29]. They also have similar flight behavior and feed on pollen and nectar [30, 31]. This type of mimicry is called Batesian mimicry because the mimic, although it is not dangerous to predators, benefits because the model is dangerous to predators [32]. In other words, predators may avoid bees because they can inject toxins by stinging, so predators also avoid such flower flies (*Eristalis* spp.) due to similarities with bees [33]. Therefore, from the perspective of pollination the acanthaceous plant species exhibit a morphological specialization of its flower due to- **i.** formation of tube; **ii.** concealment of nectar within the tube **iii.** residency of pollen on the pollinator is influenced by the geometry of the flower and the capacity of flower to familiarize the pollinator repeatedly and to achieve precise and accurate pollen placement on, and receipt from, the animal (nototribic). Hence, specific ecological niche with complex floral morphology may lead the shifting of typical melittophily to syrphid myophily in *Ecbolium ligustrinum*.

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