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Facultative myrmecophily in *Deudorix isocrates* (Fabricius) (Lepidoptera: Lycaenidae)

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Abstract

The present study investigated the interactive, apparently mutualistic relationships between caterpillars of *D. isocrates* and different ant species in pomegranate orchard (cv. Bhagwa) at the ICAR-Indian Institute of Horticultural Research (IIHR), Bengaluru during 2013-14. The larvae secreted a sugary substance from the dorsal nectary organ on the 7th abdominal segment and the tending ants were noticed to feed upon the secretion. In return, the tending ants were noticed carrying the larval frass to the outside of the bored hole. *Camponotus compressus* Fabricius was the most commonly observed (34.14%) of seven different ant species that interacted with *D. isocrates* larvae. The present study observed tending ants walking around the larval entry hole, entering the hole, bringing out larval frass from inner feeding gallery to outside of the fruit and interacting with other tending ants. Further, only advanced stages of larval damage on pomegranate fruit attracted ant attention. The intricacies involved in *D. isocrates* larva and tending ants are discussed in detail.

Keywords: *Punica granatum*, lycaenid larva-ant association, behavioural events

Introduction

'Myrmecophily', an ability to establish symbiotic relationship with ants is an ancestral character among the butterfly members of family Lycaenidae (Lepidoptera) usually referred as the 'blues', 'coppers', 'hairstreaks', 'metal marks' etc [1]. The larval stages of these butterflies associate with ants, and the intimacy of these associations is defined by the degree of dependence on the ant partner [2]. The degree of association with ants varies from facultative, unspecific to obligate, species-specific interactions between lycaenid larvae and ants [3, 4].

Several lycaenid butterflies are pesteriferous on cultivated crops during their larval stage and can cause significant losses. *Deudorix isocrates* (Fab.) (Lepidoptera: Lycaenidae) is an economically important pest in India and is found wherever pomegranate is grown. The *D. isocrates* caterpillars provide a remarkable exception because they are into stable associations (myrmecophily) with ants like any other lycaenid caterpillars. The strength of lycaenid – ant associations is variable and ranges from loose, facultative unspecific relationships to strictly obligate associations [5]. More than three-quarters of lycaenid species associate with ants during their development and vary in their dependence on the ant partner [2, 6, 7]. Little is known about the relationship between *D. isocrates* caterpillars and their associated ants. We here present a study on myrmecophilous interactions between larvae of *D. isocrates* and the different ant species. Specifically, we addressed the functions and purpose of different organs of *D. isocrates* caterpillar associated with ants interaction; behavioural events involved in ant-lycaenid larva interactions; identification of different ant species which are interacted with caterpillar and finally type of interaction that exists.

Materials and Methods

Studies on ant-lycaenid interactions were conducted to understand the mutualistic relationship between *D. isocrates* larvae and associated ants in an eight year old pomegranate orchard (cv. Bhagwa) at the Indian Institute of Horticultural Research (IIHR), Bengaluru (12° 58' N; 77° 35' E), Karnataka, India between 2013-14.

The lycaenid borer, *D. isocrates* infesting pomegranate fruits were tagged and continuously monitored for ant association and movement (n = 15). We recorded the presence of ant associates, number of ants tending the lycaenid larva, plant stem girth (cm), infested fruit circumference (cm), larval feeding hole diameter (cm), number of ants (ant traffic) on -

infested fruits, - neighboring shoots and -whole plants. The extent of *D. isocrates* larval damage on fruit was visually graded on a scale of 1-3 based on the hole size and texture of the larval frass, where 1 = fresh pinhead size entry hole (0.1 - 0.2 cm diameter) without any larval frass, 2 =later stage infestation with bigger entry hole (0.2-0.3 cm diameter) with fine saw dust like larval frass and 3 =advanced stage lycaenid larval infestation with large entry holes (>0.4 cm diameter) with big granular larval frass.

The behavioral sequences of randomly chosen ant-lycaenid interactions were monitored continuously until tending ants moved from the lycaenid larval feeding hole. The time taken for each activity was recorded using a digital clock. Data on the sequence of ant-lycaenid associations in different interaction episodes (n = 13) were compiled to construct behavioral ethogram of most common interaction (with two tending ants) considering major behavioral components, frequency, flow duration and pattern of tending ant behavior. The mean time spent in each activity and mean frequency of each behavior exhibited was calculated. Here the transitional behaviors that preceded/succeeded the ants entry/exit in to larval feeding hole alone were included. Ants tending the larvae were collected in 70% ethyl alcohol for identification.

Laboratory observations were also made to understand lycaenid-ant association. Lycaenid infested pomegranate fruits with tending ants were brought to the laboratory immediately with minimal disturbance of the surrounding environment and carefully placed under a stereomicroscope (40X) for 15 min to allow usual interaction to take place. Then the fruits were cut open gently with scalpel to view the behavioral interaction happening between ants and lycaenid larva.

Statistical analyses

The data are characterized using descriptive statistics/frequencies (mean and standard error) to visualize the behavioral profiles of ant-lycaenid interaction. Further, correlation and regression analyses between different traits involved in ant-lycaenid interaction were carried out. A step-wise regression was attempted to identify potential sets of significant explanatory variables influencing ant-lycaenid interactions [8].

Results and Discussion

Association of different ant species with pomegranate fruit borer, *D. isocrates* larvae

Observations revealed that seven species of ants tend *D. isocrates* larvae: common godzilla ant, *Camponotus compressus* (Fab.), carpenter ant, *Camponotus parius* (Emery), short legged hunch backed ant,*Myrmicaria brunnea* Saunders, the long horn crazy ant, *Paratrechina longicornis* (Latreille), *Monomorium* sp., *Lophomyrmex quadrispinosus* (Jerdon), *Phiedole* sp. were found associated with larvae of *D. isocrates*. Nevertheless, the degree of association differed among the ant species. *Camponotus compressus* was the most commonly observed species (35.14%) tending the *D. isocrates* larva, followed by *C. paria* (18.92%), *M. brunnea*, *Monomorium* sp. (13.51%), *L. quadrispinosus*, and *P. longicornis* (8.11%). These results are in accordance with, there are 21 ant genera from the three subfamilies: Myrmicinae, Formicinae and Dolichoderinae found in association with 98 lycaenid butterfly species [14]. In the present study, of several species of ants, *C. compressus* was found to be the dominant species (35.14%) tending the *D. isocrates* larva, followed by *C. paria* (18.92%). *Camponotus* species are reported as the most frequent ant associates with another lycaenid, the Miami blue butterfly, *Cyclargus thomasi bethunebakeri* (Comstock & Huntington) larvae also [15].

Nature and type of ant association with lycaenid larvae, *D. isocrates*

The relationship between the ants and the lycaenid larva appeared to be mutualistic. Close monitoring revealed that the ants provided transportation services by removing larval frass to outside of the bored hole, in return the larva provided presumably nutritional sugary substance secreted by its Dorsal Nectary Organ (DNO) to the tending ants (Fig.1a).The larval feeding hole, plugged with frass was partially cleared by the tending ants in an attempt to get the sugary substance secreted by the lycaenid. Detailed observations under a stereomicroscope revealed that lycaenid larvae secreted a droplet from the Dorsal Nectary Organ (DNO) on the seventh abdominal segment of the larva (Fig.1a) when approached by an ant. The approaching ant immediately ate down the droplet, exited the feeding hole, and cleaned its antennae with its mouthparts (Fig. 1c, d). During this process, a pair of white, tubular tentacular organs with fine setae situated on the 8th abdominal segment was also found actively protracting out, and seemed to be releasing either acoustic or volatile chemicals signals to attract the tending ants from outside the feeding hole (Fig.1b). Earlier studies also confirmed that tending ants can derive nutritive benefits by tending myrmecophilous lycaenid caterpillars of other species [9-11]. Lycaenids producing particularly valuable secretions would be expected to maintain a larger cadre of dominant, aggressive tended ants than those producing less valuable secretions [12].The nutritive secretion from DNOs (dorsal nectary organ) was reported to contain carbohydrates like sucrose, glucose, arabinose, fructose, maltose, trehalose and lactose, different free amino acids and trace amounts of methionine [2,13].

Usually, the number of lycaenid larval feeding holes per fruit ranged between 1-2 and the number of ants guarding each feeding hole ranged from 1 to 3 (Table 1, Fig.2).However, the relative occurrence of two tending ants for each lycaenid feeding hole is found to be the most common criterion (Fig. 2). When two lycaenid feeding holes exists on the same fruit, the ants guarding these holes were found to be interchanging quite often between feeding holes.

Behavioral inventory of tending ants associated with lycaenid larva

Different behavioral events exhibited by the tending ants during their interaction with lycaenid larvae can be enumerate as: 1) walking around the larval entry hole; 2) peeping into the larval entry hole; 3) waiting near the hole; 4) entering the hole; 5) cleaning mouthparts with foreleg after exiting the hole; 6) bringing out larval frass from the feeding gallery to outside of the fruit; 7) and interacting with conspecific ants. Several times, the tending ants that entered the larval feeding hole exit cleaning their mouthparts symbolizing wiping mouthparts after having the meal (here sugary secretion from the larva) (Fig.3).

The total time the tending ants interacted with lycaenid larva ranged from 28.50 - 82.50 min across the observed ant-lycaenid interaction episodes. The total time the tending ants spent within the feeding hole ranged from 10.08 - 30.5 min and each stay of tending ant in the hole ranged between 1.15 - 6.0 min. The number of entries by tending ants in to the larval hole ranged from 4.0 - 8.0 with a mean of 4.7 ±0.23 (for tending ant I) and from 3.0 - 5.0 with a mean of 4.17 ±0.17 (for tending ant II). Similarly the number of exits from larval hole ranged from 3.0 to 7.0 with a mean of 4.17 ±0.24 (for tending ant I) and from 3.0 - 8.0 a mean of 4.64 ±0.3 (for tending ant II).There was a significant difference for the mean number of entries (*P*=0.02) as well as exits (*P*=0.03) among the tending ants, tending ant I and II. Nevertheless, there is no significant difference between tending ants for time spent inside the hole (min), time spent outside the hole (min), numbers of peeping in to the hole when the fellow ant stays inside, cleaning the mouth parts (a symbol of having the meal inside the hole) and frequency of transporting larval frass from feeding hole to outside. The behavioral ethogram representing behavioral sequences that are observed during different ant-lycaenid interaction in different episodes are presented in Fig 4 and Table 1.

Descriptive statistics and correlation analysis of ant-lycaenid interaction

The observations recorded on *D. isocrates* infested fruits to understand ant-lycaenid interactions revealed that the mean circumference of fruits infested by lycaenid ranged between 9 - 27 cm with a mean of 19.19 ±0.17 cm. The diameter of the hole made by the lycaenid larva ranged from 0.1 - 0.6 cm with a mean of 0.22 ±0.01 cm. The ant traffic observed on the -whole plant, -shoots and -infested fruits ranged between 0.00 to 40.00 with a mean of 10.22 ±0.65; 0.00 - 40.00 with a mean of 9.85 ±0.63 cm; and 1.00 - 3.00 with a mean of 1.51 ±0.04, respectively. The degree of larval damage on the fruits where ant-lycaenid interactions were noticed ranged between 1.00 - 3.00 with a mean of 1.50 ±0.04 (Table 2).

The correlation analysis of different parameters involved in ant–lycaenid interaction: Ant traffic on the whole plant was significantly ($p = 0.05$) and positively correlated with ant traffic on infested fruits ($r = 0.31$), ant traffic on shoots ($r = 0.98$), presence of tending ants ($r = 0.21$), and body size of tending ants ($r = 0.22$). Ant traffic on neighboring shoots is significantly ($p = 0.05$) and positively correlated with ant traffic on infested fruits ($r = 0.27$) and body size of tending ants ($r = 0.19$). Further, ant traffic on infested fruits is also found to be significantly ($p = 0.05$) and positively correlated with degree of lycaenid damage ($r = 0.31$), presence of tending ants ($r = 0.64$) and body size of tending ants ($r = 0.66$). The degree of lycaenid damage is found to be significantly ($p = 0.05$) and positively correlated with presence of tending ants ($r = 0.37$) and body size of tending ants ($r = 0.39$).Presence of tending ants and body size of tending ants is also found to be significantly ($p = 0.05$) and positively correlated ($r = 0.94$). The larval entry hole diameter was found to be significantly ($p = 0.05$) and positively correlated with ant traffic on infested fruits ($r = 0.26$), degree of lycaenid, *D. isocrates* damage on fruits ($r = 0.90$), presence of tending ants ($r = 0.30$) and body size of tending ants ($r = 0.32$).

Relationship of ant movement with various parameters

Ant traffic on the whole plant: Variability in ant traffic on the whole pomegranate plant can be explained to the tune of 98% with ant traffic in neighboring shoots itself. However, addition of other variables, ant traffic on infested fruits, presence of tending ants, body size of tending ants could not improve the R^2 value over and above (Table 3).

Ant traffic in neighboring shoots: Variability in ant traffic on neighboring shoots explained 4-7% (Table 4).

Ant traffic on infested fruits: Variability in the ant traffic found on *D. isocrates* infested fruits can be explained to the tune of 41% by the presence of tending ants on fruit alone. The larval entry hole diameter, ant traffic in whole plant, ant traffic in neighboring shoots, degree of lycaenid damage individually could explain the variability in ant traffic on infested fruits to the extent of 7, 10, 7 and 10% respectively. The stepwise regression of different variables could not improve the R^2 value over and above 49 per cent (Table 5).

Presence of tending ants: The maximum variability in the presence of tending ants on infested fruits could be explained to the tune of 40% by the observed ant traffic on infested fruits itself. Stepwise regression of different variables could improve the R^2 up to 44% only (Table 5). The larval entry hole diameter, ant traffic on whole plant, degree of lycaenid damage could explain the variability in the presence of tending ants on *D. isocrates* infested fruits to the tune of 10, 4, and 14% respectively. The body size of tending ants was found to depend on larval entry hole diameter and degree of lycaenid damage as these two variables could explain the variability up to 10 and 15% respectively.

The correlation analysis of different parameters involved in ant–lycaenid larval interaction revealed that ant traffic on infested fruits is found to be significantly (p=0.05) and positively correlated with degree of lycaenid damage (r=0.31). This clearly shows that only advanced stages of larval damage attract ant attention. Further, ant traffic on infested fruits alone could explain the presence of tending ants up to 40%. This shows that all ants that are moving on infested fruit are likely involved in lycaenid interaction. However, the ant traffic in whole plant could explain the presence of tending ants only to the tune of 10% implying all ants present on the pomegranate plant are not involved with lycaenid larval interaction. Further, the lycaenid larval related variables, larval entry hole diameter (10%), degree of lycaenid damage (14%) also could explain the presence of tending ants to limited extent only. This clearly shows that a very weak facultative ant association exists between pomegranate fruit borer, *D. isocrates* larva and tending ants. Previous studies also reported that most lycaenid butterfly species interact with ants, and many of these relationships include substantial benefits for lycaenid larvae [7]. However, the costs and benefits of ant tending for myrcophilous lycaenids may vary substantially from facultative to obligate relationships [16-19].

Further, there is no constant interaction between the lycaenid larva and the tending ants. The observed interaction lasted for short duration ranging between 9.15 to 30.50 min and the associated ants dispersed in to nearby shoots. Such facultative associations are commonly encountered between ants and lycaenids, although the nature and patterns of associations are typically unclear. Previous studies also reported a facultative symbiosis involving the lycaenid larva *Thelinesthes albocincta* (Waterhouse), its host plant *Adriana quadripartite* (Labill.) Muell.Arg. and native Australian ants [20]. These data suggest that the relationship between *D. isocrates* and its attending ants is facultative.

Table 1: Behavioral events of tending ants associated with lycaenid larva

Associated behaviors	Tending ant I			Tendingant II		
	Mean± SE	**Min**	**Max**	**Mean± SE**	**Min**	**Max**
Time spent inside hole (min)	14.93±1.08	10.8	30.5	13.77±0.82	8.7	23.0
No. of entries	4.70±0.23	4.0	8.0	4.17±0.17	3.0	5.0
Time spent outside hole (min)	13.92±0.87	8.7	23.0	15.08±1.11	9.8	30.5
No. of exits	4.17±0.24	3.0	7.0	4.64±0.30	3.0	8.0
Peeping in to hole (No.)	5.52±0.64	2.0	10.0	5.82±0.57	1.0	9.0
Interaction with other ants (No.)	0.70±0.11	0.0	1.0	0.70±0.11	0.0	1.0
Cleaning while exiting (No.)	0.94±0.15	0.0	2.0	0.76±0.18	0.0	2.0
Cleaning after throwing frass (No.)	0.35±0.11	0.0	1.0	0.58±0.0.14	0.0	2.0

Table 2: Descriptive statistics of ant-lycaenid larval interactions

Parameter	Mean±SE	Minimum	Maximum
Plant stem girth (cm)	18.76±0.11	13.00	24.50
Larva exit hole diameter (cm)	0.22±0.01	0.10	0.60
Ant- traffic			
- On whole plant	10.22±0.65	0.00	40.00
- On shoots	9.85±0.63	0.00	40.00
- On infested fruits	0.29±0.03	0.00	3.00
Larval damage*	1.51±0.04	1.00	3.00

* Ant-lycaenid interaction on damaged fruits

Table 3: Relationship between ant traffic in whole pomegranate plant with various parameters

Variables	Regression equation	R^2
Ant traffic in whole plant Vs.		
a. Ant traffic on neighboring shoots	$y = 0.30+1.01x_5$	0.98
b. Ant traffic on infested fruits	$y = 8.63+5.32x_6$	0.10
c. Presence of tending ants	$y = 9.61+7.69x_8$	0.04
d. Body size of tending ants	$y = 9.55+5.57x_9$	0.05
e. Ant traffic on neighboring shoots, infested fruits, presence of tending ants together, body size of tending ants	$y = 0.18+0.99x_5+0.74x_6+0.08x_8+0.20x_9$	0.98
f. Ant traffic on neighboring shoots, infested fruits, presence of tending ants together	$y = 0.18+0.99x_5+0.75x_6+0.33x_8$	0.98
g. Ant traffic on neighboring shoots, infested fruits,	$y = 0.18+0.99x_5+0.85x_6$	0.98

Table 4: Relationship between ant traffic in neighboring shoots with various parameters

Variables	Regression equation	R^2
Ant traffic in neighboring shoots Vs.		
a. Ant traffic on infested fruits	$y = 8.51+4.51x_6$	0.07
b. Body size of tending ants	$y = 9.30+4.65x_9$	0.04
c. Ant traffic on infested fruits, body size of tending ants	$y = 8.52+4.25x_6+0.57x_9$	0.07

Table 5: Relationship of tending ants with various parameters

Variables	Regression equation	R^2
Presence of tending ants Vs.		
a. Larval entry hole diameter	$y =-0.06+0.64x_3$	0.10
b. Ant traffic in whole plant	$y =0.02+0.01x_4$	0.04
c. Ant traffic on infested fruits	$y =-0.01+0.29x_6$	0.40
d. Degree of lycaenid damage	$y =-0.15+0.15x_7$	0.14
e. Larval entry hole diameter, ant traffic in whole plant, ant traffic on infested fruits, degree of lycaenid damage	$y =-0.13-0.18x_3 + 0.0001x_4+0.26x_6+0.10x_7$	0.44
f. Larval entry hole diameter, ant traffic in whole plant, Ant traffic on infested fruits	$y =-0.08+ 0.31x_3+0.001x_4+0.28x_6$	0.43
g. Larval entry hole diameter, ant traffic in whole plant	$y =-0.12+ 0.63x_3+0.01x_4$	0.13
h. Larval entry hole diameter, degree of lycaenid damage ant traffic in whole plant	$y =-0.21-0.32x_3+0.02x_7 +0.01x_4$	0.18
i. Larval entry hole diameter, degree of lycaenid damage	$y =-0.16-0.32x_3+0.20x_7$	0.14
j. Larval entry hole diameter, ant traffic on infested fruits	$y =-0.07+0.31x_3+0.28x_6$	0.43
Body size of tending ants Vs		
Larval entry hole diameter	$y=-0.10+1.00$	0.10
Degree of lycaenid damage	$y=-0.23+0.23$	0.15
Larval entry hole diameter, degree of lycaenid damage	$y=-0.24-0.43+0.30$	0.15

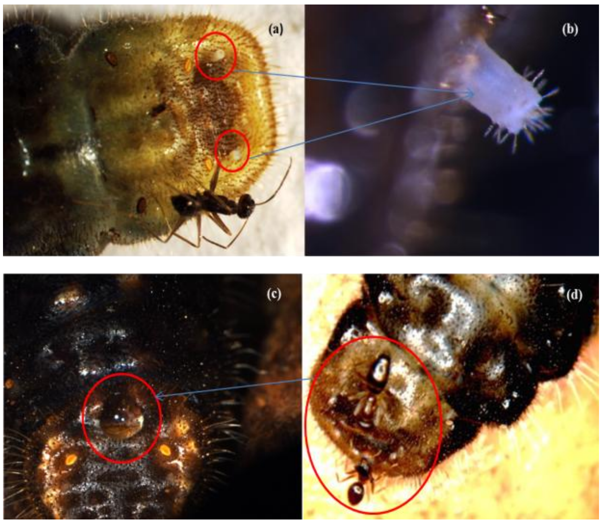

Fig 1: Lycaenid-ant interacion (a) pair evesible tentacle organs attracting ants, (b) Microscopic view of tentacle organs, (c) nutritive droplet from Dorsal Nectary Organ (DNO), (d) Two ant harvesting the droplet from DNO.

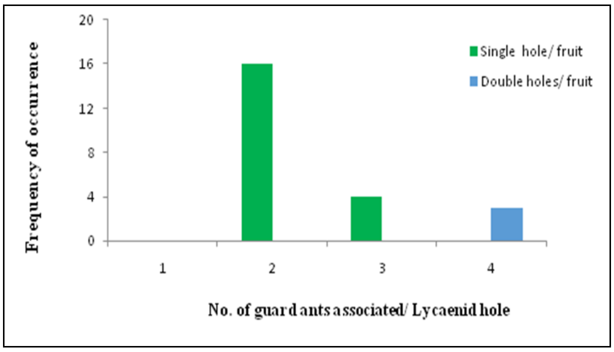

Fig 2: Association of guard ants with different larval feeding holes per fruit

Fig 3: Ants tending pomegranate borer infested fruits; (a) ants foraging on pomegranate, (b) tagging of borer infested fruits, (c) one ant entering into hole and another ant waiting outside, (d) single ant interaction with larva, (e) single ant waiting near bored hole.

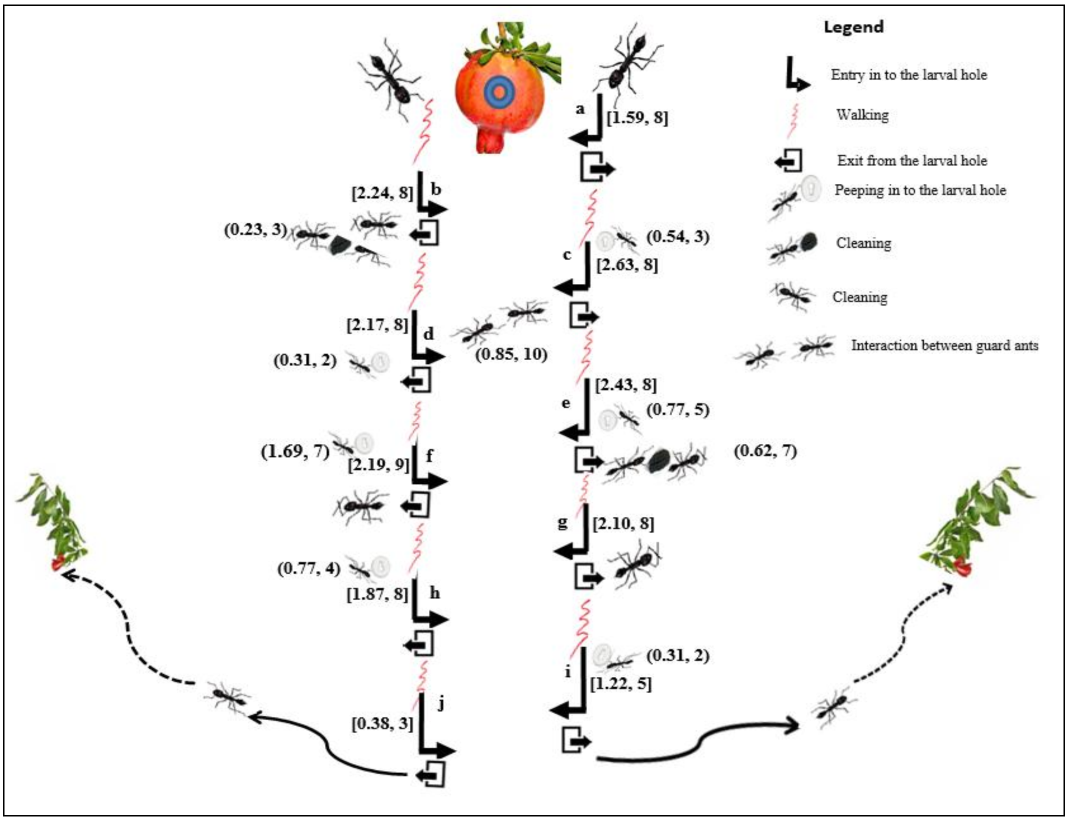

Fig 4: Ant-lycaenid interaction behavioral ethogram: two guard ants tending lycaenid larva. Figures in parenthesis [Mean, Frequency] shows time spent (minute) in particular activity; figures in parenthesis (Mean, Frequency) shows frequency (Number) of particular activity; alphabets denotes the sequential order of behavioral activity.

Conclusion

The Lycaenidae provide a model system for studying the evolution of complex species interactions. The butterfly larvae were noticed releasing nutritional substances to attract the ants. In return, ants provided protection from predation, parasitism and cleaning (avoid the plugging of hole with excreta by the borer). In depth understanding of the development, ecological chemistry, function and evolution of ant – lycaenid interaction is urgently required to exploit this symbiotic relationship for this lycaenid management.

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