‘Mother knows best’: oviposition behaviour in insects

By

Beegam Salma M.P.

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DEPARTMENT OF AGRICULTURAL ENTOMOLOGY
COLLEGE OF HORTICULTURE
KERALA AGRICULTURAL UNIVERSITY
VELLANIKKARA - 680656
THRISSUR

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CERTIFICATE

This is to certify that the seminar report entitled **"Mother knows best: oviposition behaviour in insects"** has been solely prepared by **Beegam Salma M.P. (2018-11-117)**, under my guidance and has not been copied from seminar reports of any seniors, juniors or fellow students.

Vellanikkara

25.01.2020

Dr. Vidya C.V.
(Major Advisor)
Assistant Professor
Agricultural Entomology
College of Agriculture, padannakad

DECLARATION

I, Beegam Salma M.P. (2018-11-117), hereby declare that the seminar entitled "**Mother knows best: oviposition behaviour in insects"** has been completed by me independently after going through various references cited at the end and I have not copied from any of the fellow students or previous seminar reports.

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Beegam Salma M.P.
(2018-11-117)

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Certified that the seminar report entitled **"Mother knows best: oviposition behaviour in insects"** is a record of seminar presented by **Beegam Salma M.P. (2018-11-117)** on 15th November, 2019 and is submitted for the partial requirement of the course ENT 591.

Dr. Anil Kuruvila
Professor
Department of Agricultural Economics
College of Horticulture, Vellanikkara

Dr. Reshmy Vijayaraghavan
Assistant Professor
Department of Plant Pathology
College of Horticulture, Vellanikkara

Dr. Sangeeta Kutty M.
Assistant Professor
Department of Vegetable science
College of Horticulture, Vellanikkara

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1. Introduction

The existence of all living organisms on earth ultimately decided by its reproductive success. However various biotic and abiotic stress that thrust to the survival of offspring. To overcome this, parent spends considerable time and energy and protects their offspring. Insects are also not an exception to this. In insects, the first stage of development is the egg stage, which is immobile and very much vulnerable to number of stresses. Hence the decision of mother insect largely determines the success of insect on earth.

Oviposition is the process by which egg passes from the external genital opening or vulva of the female insect to the outside (Gullan and Cranston, 1994). Insects oviposit either directly through gonopore, which is present behind the eighth or ninth abdominal segment or through a specialized structure called ovipositor. Insects such as butterflies, moths and beetles lay eggs directly through gonopore, whereas grasshoppers, crickets and many parasitic wasps lay eggs using ovipositor.

Oviposition through gonopore

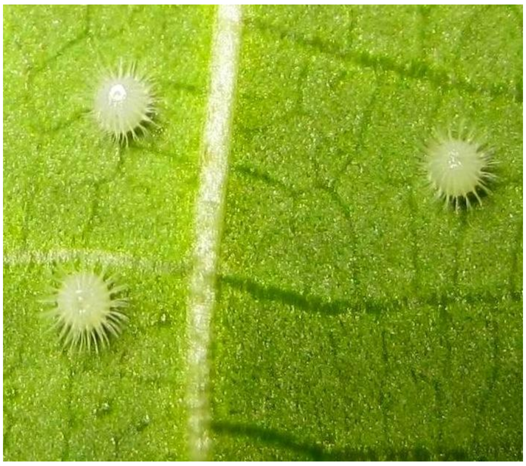


Plate 1. Egg of castor butterfly

Plate 2. Eggs of stink bug

Oviposition using ovipositor

Plate 3. Ovipositor of grasshopper

Plate 4. Ovipositor of ichneumonid wasp

In many insects female accessory glands are well developed. The secretion of these glands covers or protects the eggs and also helps to escape from predation. Eg: nit in head louse and pedicellate eggs in green lacewings. Whereas in cockroaches it act as a protective shield called ootheca. In yellow stem borer after laying eggs they cover eggs with hairs, it is also a female accessory gland secretion.

Plate 5. Egg mass of yellow stem borer

Plate 6. Nit in head louse

Plate 7. Ootheca of cockroach Plate 8. Pedicellate eggs of green lacewings

2. Where do insect oviposit?

In some insects both adults and offsprings feed on the same food and live in same habitat. Here the female insect will oviposit in the place where parent sustain. eg: nymphs and adult of redcotton bug.

In many insects the larvae and adult feed on different food and live in different habitat. Eg: citrus butterfly. Certain insects, though they feed on same plant adult and larvae prefer different part of the plant eg: pollu beetle. In such cases ovipositional preference may be either to increase the survival of their offspring or to increase their own longevity.

Oviposition preference of mother insect can be explained by two hypotheses

I. Mother knows best hypothesis
II. Optimal bad motherhood hypothesis

a) **Mother knows best hypothesis**

Also termed as Preference - performance hypothesis. According to this hypothesis, female prefer to oviposit on a place where which is best suitable for the offspring development. Female maximizes the fitness by optimizing offspring performance and Host preference patterns are also shaped by offspring performance (Mayhew, 1997).

2.1 Host choice of chrysomelid beetle, *Cephaloleia* spp.

Commonly known as rolled leaf beetles, are the native of Neotropics. Host of these beetles includes Zingiberales (ginger, turmeric, *etc*). Due to the introduction of exotic Zingiberales into rainforest of South Costa Rica, beetles expanded their host range to this exotic Zingiberals. (Garcia-Robledo and Horvitz, 2012) they studied the Ovipositional preference of two species *Cephaloleia belti* and *Cephaloleia placida* on native and novel host plants. In case of *Cephaloleia belti* native host is *Heliconia latispatha* and novel host is *Musa velutina*. For *Cephaloleia placida* native host is *Renealmia alpinia* and novel host is *Alpinia purpurata*. They found that, larval acceptability and larval survival of two beetles more in native host than novel host. Whereas adult preference and adult longevity is more in novel host than native host. Even then ovipositional preference of adult female beetle is more in native than novel host, because the larval survival of two species of *Cephaloleia* are more in native host. Hence they proved that Optimization of offspring performance determines host choice.

Table 1. Larval acceptability and larval survival of *Cephaloleia* spp. on native and novel host plants

Species	**Native host**	**Novel host**	**Larval acceptability**	**Larval survival**
C. belti	*Heliconia latispatha* (**HL**)	*Musa velutina* (**MV**)	**HL>MV**	**HL>MV**
C. placida	*Renealmia alpinia* (**RA**)	*Alpinia purpurata* (**AP)**	**RA>AP**	**RA>AP**

Table 2. Ovipositional preference of *Cephaloleia* spp. on native and novel host plants

Species	Native host	Novel host	Adult preferences	Adult longevity	Oviposition preference
C. belti	*Heliconia latispatha* (**HL**)	*Musa velutina* (**MV**)	**HL<MV**	**HL<MV**	**HL>MV**
C. placida	*Renealmia alpinia* (**RA**)	*Alpinia purpurata* (**AP**)	**RA≥AP**	**RA=AP**	**RA>AP**

b) Optimal bad motherhood hypothesis

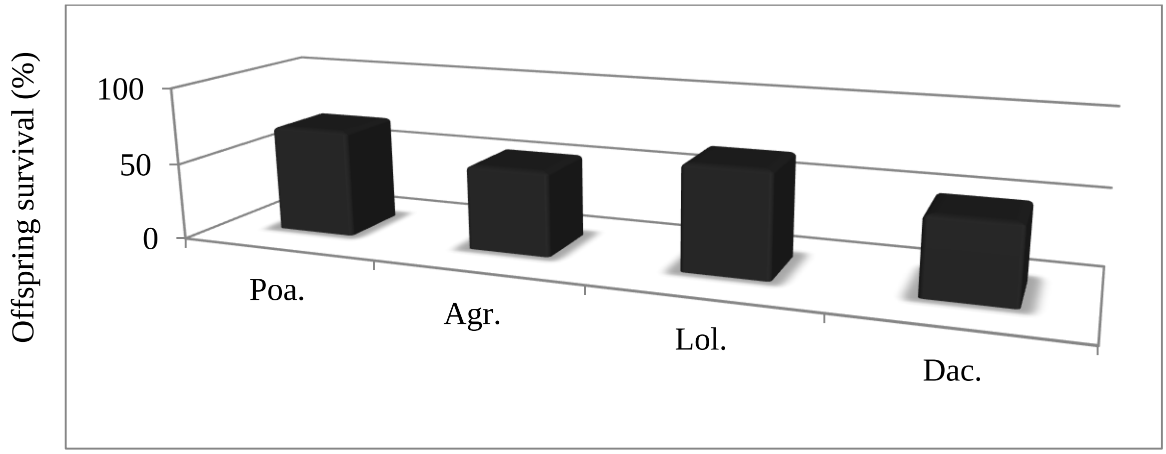
According to this hypothesis, host plant that maximizes the survival of offspring may not increase the longevity of adult. Here female will increase the fitness by increasing their own performance and they will decide the host for oviposition based on the performance of adult not the offspring preference.

2.2 Host choice of grass miner, *Chromatomyia nigra*

It is an oligophagous leaf miner, feed on different species of grasses. Here female insert their eggs into the leaf tissue and adult female feed on the exuding sap coming out of the oviposition punctures.

Scheirs *et al*. (2000) studied the offspring and adult performance of *Chromatomyia nigra* on four different types of grasses includes *Poa trivialis, Lolium perenne, Agrostis tennuis* and *Dactylis glomerata*.

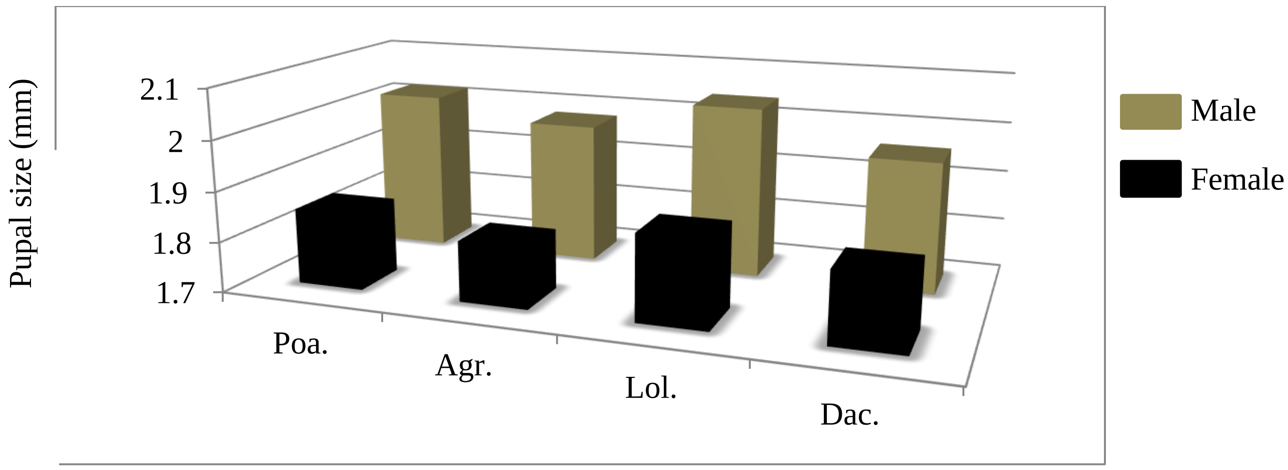
Fig 1. Offspring performance of *Chromatomyia nigra*



Grass species

Poa. –*Poa trivialis*, **Lol.**–*Lolium perenne,* **Agr.**–*Agrostis tennuis,* **Dac.** –*Dactylis glomerata*

Fig1.2 Pupal size of offspring of *Chromatomyia nigra*



Grass species

It was found that the offspring survival and pupal size more or the grass *Lolium perenne* and but the adult showed more performance towards the grass species *Poa trivialis*

Fig 2. Adult performance of *Chromatomyia nigra*

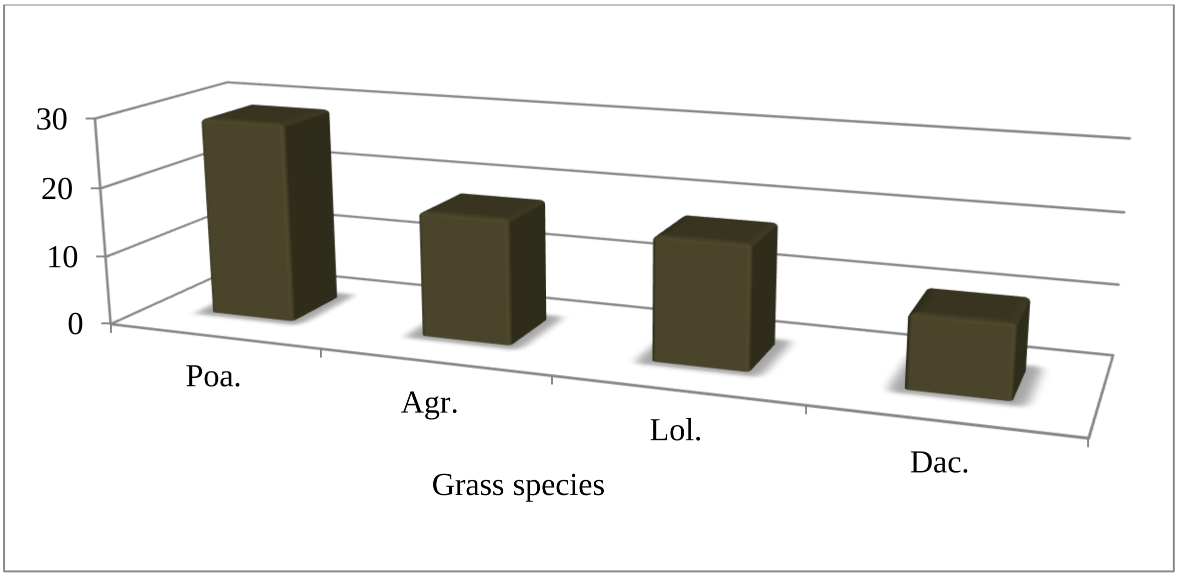


Fig 3. Feeding preference of adult *Chromatomyia nigra*

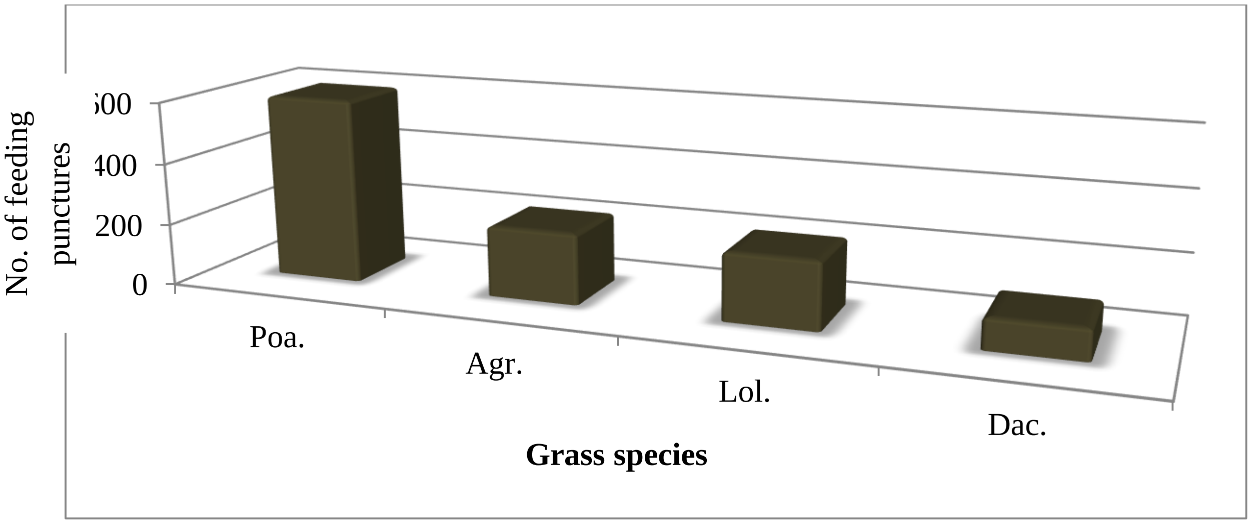
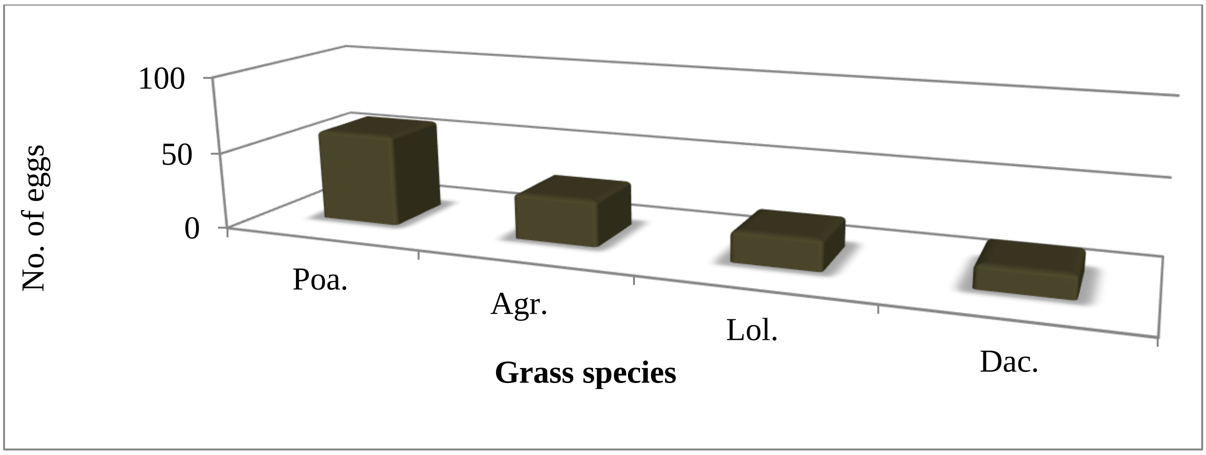


Fig 4. Oviposition preference of *Chromatomyia nigra*



Scheirs *et al*. (2000) studied the adult performance and oviposition preference in four different grass species. It was found that more number of eggs and feeding punctures more in the grass *Poa trivialis*. Here female prefer to oviposit on the plant that maximize her fitness. Hence they proved that adult performance determine the host choice.

3. Host selection by insects for oviposition

There are different steps involved in host selection by insects, for finding their appropriate site for oviposition these includes, host habitat finding, host finding, host recognition and finally host acceptance. In host selection female show a sequence of behaviour which ultimately leads to the host for oviposition. At every step female insect uses different cues or stimuli from the host habitat or from the host for finding their host for oviposition.

3.1 Host habitat finding

In this step adult insect makes an oriented movement towards the host habitat. This is the critical step, which can guarantee the survival of both eggs and larvae. To find the host habitat mother uses both chemical and visual stimuli. Many insects' uses light as visual cues for host habitat finding. Whereas chemical stimulus includes plant volatiles, HIPVs, volatiles from plant-host complex.

3.1.1 Visual stimuli - dragonfly (*Aeshna juncea* and *Orthetrum brunneum*)

Dragonflies prefer either 'dark' or 'bright' water (as perceived by the human eye viewing downwards perpendicularly to the water surface), while others choose both types of water bodies in which to lay their eggs. Certain dragonfly species may select their preferred breeding sites from a distance on the basis of the polarization of reflected light. That waters viewed from a distance can be classified on the basis of the polarization of reflected light. Usually mayflies and dragonflies prefer to oviposit on water. A distance, at which the angle of view is 20 degree from the horizontal, dark water bodies, cannot be distinguished from bright ones on the basis of the intensity or the angle of polarization of reflected light. At a similar angle of view, however, dark waters reflect light with a significantly higher degree of linear polarization than bright waters in any range of the spectrum and in any direction of view with respect to the sun. One of dragonfly species *Aeshna juncea* they prefer to oviposit on dark water. While another species *Orthetrum brunneum* prefer to oviposit on bright water. They use polarization of reflected light as stimuli for oviposition (Bernath *et al.,* 2002). Because the ventral side of dragonflies eyes are very sensitive to polarization, so they can easily find their habitat.

3.1.2 Chemical stimuli - Melon Fly Parasitoid, *Pysttalia fletcheri*

Adult female *Pysttalia fletcheri*, parasitoids of the melon fly (*Bactrocera cucurbitae*), were exposed to host-plant stimuli in a laminar airflow wind tunnel to analyze the cues used in host-habitat finding. Parasitoids hovered twice as frequently around plastic zucchini models emitting fresh cucumber odour as around models emitting clean air. The odour of decaying pumpkin was even more attractive, resulting in over an l0-fold increase in hovering, a 50-fold increase in landing, and a 150-fold increase in host-searching and probing behaviours compared to clean air. Fresh cucumber leaf odours were not attractive to the parasitoids, but decomposing leaves elicited a strong increase in hovering, landing, and searching behaviours. Plastic leaves which visually simulated cucurbit foliage did not in themselves significantly alter orientation behaviours, but the combination of leaf visual stimuli plus decaying leaf odours caused strong increases in hovering, landing, and searching behaviours. Fresh pumpkin odour and the odour of yeast-inoculated pumpkin were not as attractive to parasitoids as decaying leaf odours. Yeast isolated from decaying pumpkin and cultured on various sterile media were not substantially more attractive than clean air.

Table 3. Response of fruitfly parasitoid *Pysttalia fletcheri* to different stimuli

Stimuli	Response
Fresh cucumber	Hovering
Rotting pumpkin	Hovering, Landing, Searching
Fresh leaf odour	-
Decomposing leaf odour	Hovering, Landing, Searching

Fresh cucumber odours had only a slight effect on parasitoid behavior, indicating that fresh cucurbit volatiles may be partially attractive (resulting in increased arrestment, or hovering) but do not appear sufficient to cause the parasitoids to land. When a parasitoid moves upwind in the flight tunnel and approaches an odour emitting fruit model, this hovering behavior is usually quite distinct, and appears to be an intermediate step allowing further integration of information before the wasp makes the decision to land. In a two-step process, volatiles from fresh (undamaged) plants may help parasitoids find a suitable patch of potential host habitat, while volatiles from decaying tissues may indicate with a higher likelihood an actual host habitat, i.e., infestation by melon flies (Messing *et al*., 1996).

3.2 Host finding

After orientation process leading to host habitat. Female will land on the host. Here also female insect uses number of stimuli to locate the host. Major visual stimuli are involves shape, size and colour of the host. Chemical includes plant volatiles, kairomones, synomones and pheromones. Then also use of acoustic cues mainly mating call produced by male insects to attract opposite sex.

3.2.1 Chemical stimuli -tachinid parasitoid (*Eclytia flava*) of pentatomid bug

All tachinid larvae are obligate endoparasites of arthropods, second only in importance for biological control to parasitic Hymenoptera. Members of the four recognized tachinid subfamilies (Exoristinae, Dexiinae, Tachininae, and Phasiinae) parasitize species from ten insect orders, plus some spiders, scorpions and centipedes. Phasiines usually lay a large, so-called macro type egg on the cuticle of their host from which the larvae bore through the bottom of the egg into the haemocoel of the host. A tachinid fly *Eclytia flava* (subfamily - Phasiinae) it is an adult parasitoid of shield bug *Halyomorpha halys*. Here these bugs produce an aggregation pheromone (Methyl - 2, 4, 6 decatrienoate) that is used as a chemical cue for host finding by this tachinid fly (Aldrich *et al*., 2006).

3.2.2 Acoustic cue –*Ormia ochracea*, tachinid parasitoid of field Cricket (*Gryllus rubens*)

A tachinid fly *Ormia ochracea* (tribe Ormiini)is an adult parasitoid of *Gryllus rubens*. Gravid females of *Ormia ochracea* locate their hosts by homing on their hosts' calling songs. At Gainesville, Florida, *O. ochracea* females were attracted in greatest numbers to broadcast sounds that simulated the calling song of *Gryllus rubens* for their oviposition. The response of female *O. ochracea* to simulated *G. rubens* songs that have different pulse rates changes with temperature in parallel with temperature induced changes in the pulse rate of natural songs. The song of *G. rubens* at 21 ~ approximates a continuous sequence of 4. 6-kHz pulses at a rate of 45 s -1 and with a duty cycle of 50%. When two of these parameters were held constant and the third systematically varied in steps of 0. 4 kHz, 10 s-l, and 10-20%, maximum attraction occurred at 4. 4 kHz, 45 s -1, and 20-80% (Walker, 1993).

3.3 Host recognition

Once the host is located by the female then the next step host recognition. Female after landing will evaluate the number of sensory information by contact. In this step also uses different stimuli. Usually in butterfly use chemical stimuli to recognize host. They show different behaviour during this process like drumming with tarsal segments, tapping with antennae and probing using proboscis.

3.3.1 Gustatory stimuli - swallow tail butterfly (*Papilio xuthus*)

Swallowtail butterflies belonging to the family of Papilionidae selectively utilize a limited number of plants from a single or a few families. Female butterflies lay eggs on their host only when they detect specific chemicals through their foreleg chemosensilla while drumming on the leaf surface. Here (Ozaki *et al.,* 2011) they showed that the butterfly, *Papilio xuthus*, uses a gustatory receptor specific for synephrine to select its host in oviposition behaviour. Identified a gustatory receptor gene involved in the recognition of an oviposition stimulant, synephrine, from the *P. xuthus* by a combination of in silico, in vitro and in vivo approaches. The receptor, *PxutGr1*, responds specifically to synephrine in sf9 cells. The sensitivity of tarsal taste sensilla to synephrine and the oviposition behaviour in response to synephrine are strongly reduced after injecting double-stranded RnA of *PxutGr1* into pupae. These observations indicate that the receptor PxutGr1 represents a key factor in host specialization in *P. xuthus* (Ozaki *et al.,* 2011).

3.3.2 Non-volatile chemical - parasitic wasp *Lariophagus distinguendus* of Granary weevil (*Sitophilus granarius*)

Host recognition was examined in *Lariophagus distinguendus*, a parasitoid of larvae of the granary weevil *Sitophilus granarius* that live endophytically in wheat grains. On encountering a grain infested with *S. granarius*, females of *L. distinguendus* behave in a set sequence. First they showed antennal drumming on the grain, second they tap with the tip of the abdomen on the grain surface, and third they drill into the grain and then insert their ovipositor. Bioassays revealed that drumming and drilling was stimulated by non-volatile chemicals present on the grain-host complex. Host faeces and herbivore damaged grain material stimulated the most activity, followed by artificially damaged grain, and healthy grain. This is the first report on non-volatile chemicals released from herbivore-damaged seeds as signals for foraging parasitoids. Volatile chemicals from the faeces alone were not active. Experiments on the use of physical cues revealed that the presence of a three-dimensional structure increased the response towards chemicals from the faeces. The shape (ovoid or rectangular solid) and colour (brown or white) of the structure had no impact. Thus, physical cues alone were insufficient to stimulate host recognition behaviour, but acted by increasing the response towards the chemical stimuli (Steidle *et al*., 2000).

3.4 Host acceptance

It is the final step in host selection. In this stage female insect insert ovipositor. If find suitable accept it otherwise reject completely. This is decided by various tactile, gustatory stimuli and vibration of host.

3.4.1 Host recognition and acceptance behaviour in *Cotesiasesamiae* and *Cotesiaflavipes*

Host recognition and host acceptance behavior was studied in two species of braconid parasitoid *Cotesia sesamiae* and *Cotesia flavipes* on their host and non-hosts. These are the larval parasitoid of graminaceous stem borer. They parasitize on third and fourth instar larvae. The host of *Cotesia sesamiae* is *Busseola fusca* while that of *Cotesia flavipes* is *Chilo partellus*. *Eldana saccharina* was tried as non-host for the two parasitoids.

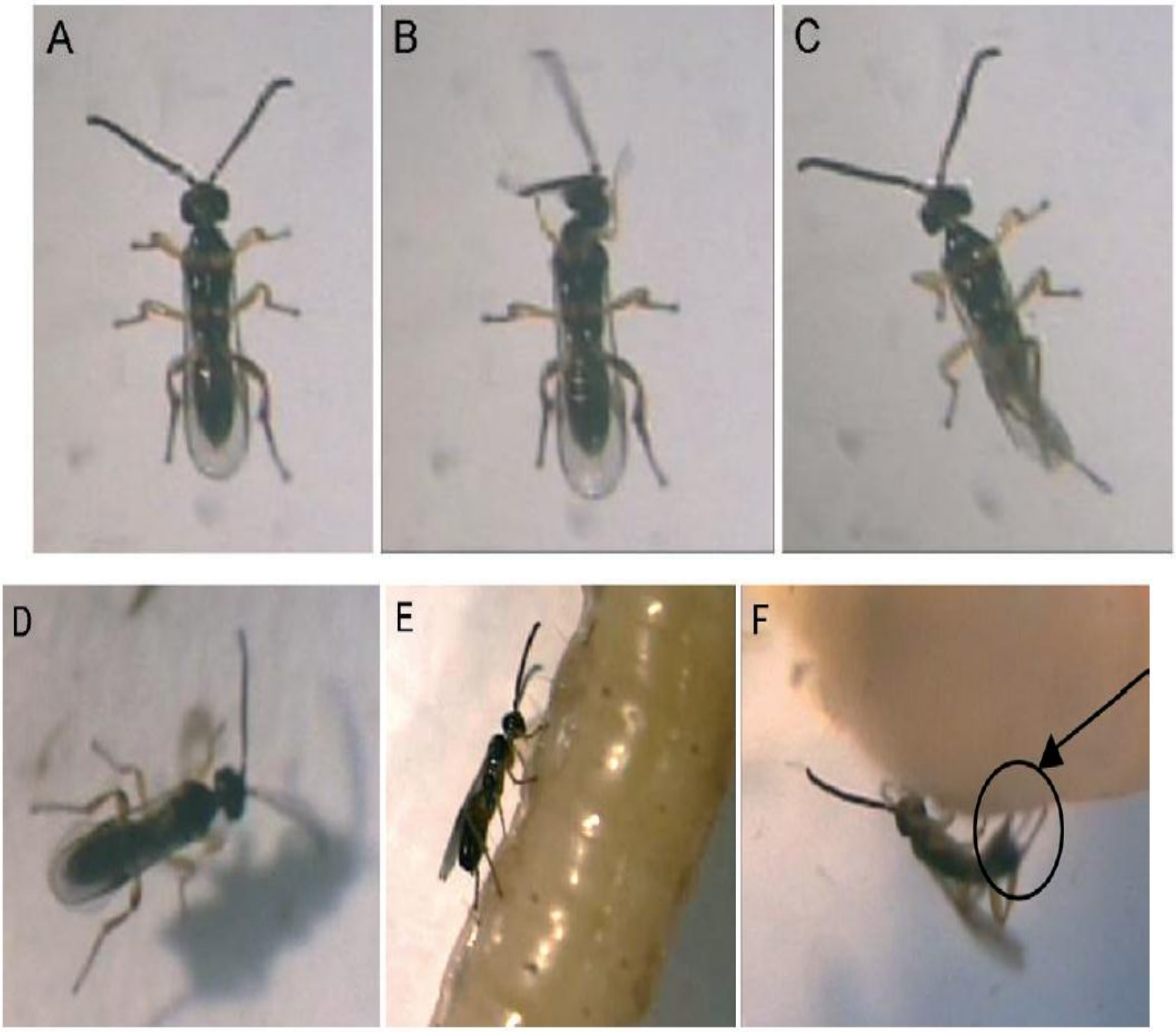
In this study, third and 4th instar larvae of stem borer species were introduced into jars containing pieces of maize and left for 24h to feed and produce frass. Then a single larva was placed in the arena. Then adult female wasp was introduced. The behaviour of female wasp for host recognition and acceptance were observed until it stung the larva or a maximum of 5 minutes. The rate of oviposition and the host larvae killed were also studied (Obonyo *et al*., 2010).

These are the behavioral steps observed before oviposition. When the wasp was introduced, it was stationary with antenna kept apart as in the first picture. This is linked with the presence of larva in the arena. This may be due to sense of odour from the larva and frass. In this phase, they cannot differentiate between smell of frass of host or non-host. This is followed by antennal grooming as shown in 2nd and 3rd picture. Then they walk in the arena while drumming the surface with the tip of antenna. Then they walk on the body of larva while drumming its surface with antenna and finally insertion of ovipositor

Time duration of each behavioural step by the wasp to three species of host. In case of both the species less time was spent for host insect, for the first two steps that is standing still and grooming, when compared to non-hosts. But there was no specific relationship between the time spent of walking on the body of insect and its preference. *C. sesamia* inserted their ovipositor only to its host, the larvae of *B. fusaca,* whereas *C. flavipes* inserted the ovipositor to its host *C. partellus* and also to non-host *B. fusca*. But both the species rejected non-host, *E. saccharina* after a stinging attempt.

Fate of host after stinging attempt or oviposition insertion 82% of the larvae of *B. fusca* were stung by *C. sesamiae*, and 52% of larvae were pupated and 16% were killed. 2% larvae were stung by *C. partellus.* Since there was no oviposition, cocoons were not formed. 62% of larvae of *C. partellus* and *B. fusca* were stung by *C. flavipes*. 46% of hosts produced cocoons. But as *B. fusca* is a non-host of *C. flavipes*, eventhough, they were stung by the parasitoid, there were no parasitoid cocoon development. Only 2% and 6% of the larvae that *C. sesamiae* and *C. flavipes*, respectively, inserted their ovipositior, but did not produce any parasitoid cocoons.

Plate 9. Behavioural steps preceding oviposition by *C. sesamiae*



A. Stationary with antenna upright and apart

B and **C**. grooming legs and /or antenna

D. Walking in the arena while drumming the surface with tip of antenna

E. Walking on the body of larva while drumming its surface with antenna

F. Ovipositor insertion

Table 4. Time duration of behavioural steps by *Cotesia sesamiae*

Parasitoid	Host tested	Duration of behavioural steps (seconds)				
		ST	G	WB	SA	O
Cotesia sesamiae	*Busseola fusca*	**16.5[a]**	**10.7[a]**	32.1[b]	0.5	**6.5[b]**
	Chilo partellus	64.5[b]	38.4[b]	**17.8[a]**	0.2	0[a]
	Eldana saccharina	24.4[b]	14.6[ab]	71.7[c]	2.4	0[a]

Table 5. Time duration of behavioural steps by *Cotesia flavipes*

Parasitoid	Host tested	Duration of behavioural steps (seconds)				
		ST	G	WB	SA	O
Cotesia flavipes	*Chilo partellus*	**17.2[a]**	**2.6[a]**	30.0[b]	**0.1**	**4.9[b]**
	Busseola fusca	31.8[a]	12.4[a]	**11.8[a]**	1.5	**5.6[b]**
	Eldana saccharina	69.7[b]	60.6[b]	37.0[b]	3.5	0[a]

ST: Standing still; **G**: Grooming; **WB**: Walking on larval body; **SA**: Stinging attempt; **O**: Ovipositor insertion

4. Challenges in host selection

Though the mother insect select their host for oviposition very carefully. She faces a number of challenges includes predation risk, competition, resource availability, tritrophic interaction *etc*. However mother finds number of ways to overcome these challenges.

4.1 Predation risk

4.2 Competition

4.3 Resource availability

4.4 Host defense

4.5 Tritrophic interaction

4.1 Predation risk

4.1.1 Avoidance

Ovipositing insects may avoid aquatic sites where there is high predation risk to their offspring, but the proximate mechanisms that mediate avoidance behaviour are poorly resolved. (Angelon and Petranka, 2002) conducted an experiment to determine whether mosquitoes would reduce oviposition rates in pools containing chemicals of the mosquito fish (*Gambusia affinis*), a voracious predator that is widely employed to control mosquitoes. Experimental treatments consisted of outdoor pools that contained known concentrations of fish chemicals (low, medium, or high) or no fish chemicals (control). The pools were arranged in a randomized block design, and the number of mosquito larvae in each pool served as the response variable to estimate relative oviposition rate. Members of the *Culex pipiens* complex were the main colonizers of the pools. The mean number of larvae per pool differed among treatments ($P = 0.026$) and was about three times greater in control pools compared with those receiving medium and high concentrations of fish chemicals. Pairwise comparisons indicate that only medium and high treatments differed significantly from controls, suggesting that a threshold concentration exists below which mosquitoes cannot reliably detect predators. Our data suggest that the effectiveness of *Gambusia affinis* in controlling mosquitoes may be compromised if adult mosquitoes respond to fish stocking by shifting to nearby breeding sites that lack fish (Angelon and Petranka, 2002).

4.1.2 Oviposition site shifting

The influence of maternal defense against natural enemies, maternal provisioning and oviposition site selection on offspring survival before and after hatching were examined in a semelparous pentatomid bug, *Ramosiana insignis*. Oviposition occurs on leaves of *Schoepfia schreberi*, or surrounding vegetation from which nymphs migrate to feed exclusively on *S. schreberi* flower buds. Oviposition is asynchronous; the mother lays additional eggs immediately prior to hatching of the core brood that rapidly consumes the additional eggs. In the absence of maternal defence egg masses were more heavily parasitized, suffered ant predation and an increased prevalence of sibling cannibalism. Maternal provisioning in the form of addition eggs significantly reduced the prevalence of sibling cannibalism of core brood eggs. Migration of the core brood away from the oviposition site was also significantly higher in the absence of maternal provisioning. If not consumed, additional eggs were capable of producing viable progeny of both sexes, indicating that they were in fact marginal progeny. The average clutch size on non-host vegetation was numerically greater than clutches laid on host trees. A greater number of additional eggs were deposited with clutches laid on non-host vegetation compared to those on the host plant. Egg masses on non-host vegetation were less likely to be discovered by parasitoids, compared to those on the host tree. Overall, clutches on non-host vegetation produced one third more offspring than clutches on the host tree. (Lopez-Ortega and Williams, 2018) conclude that *R. insignis* females present a remarkable combination of maternal defence, provisioning of additional eggs and oviposition site selection as strategies to enhance offspring survival in both the egg and nymph stages.

4.1.3 Egg dumping

Parental care can be defined as post-fertilization parental behaviour that is likely to increase offspring lifetime reproductive success, and parental care is a form of parental investment when it is costly to parents. Common benefits of parental care to offspring include protection against predators and provisioning of resources such as food. In all species of the subfamily Belostomatinae, including *Belostoma lutarium*, paternal care is provided to eggs and includes brooding an egg pad that has been deposited onto a male’s back by one or more females. Paternal care behaviour in *B. lutarium* and closely related species involves preventing desiccation of eggs by positioning the egg pad at the water surface, moving up and down at the water’s surface (i.e. brood pumping), and protection from predators by actively avoiding egg predators (Trasher *et al*., 2015).

4.1.4 Egg stacking

Seed beetle *Mimosestes amicus* may lay eggs singly, or may cover with additional eggs. This egg stacking serves to significantly reduce the mortality of the protected egg from parasitism by the parasitic wasp, *Uscana semifumipennis*. The smaller top eggs serve only as protective shields; they are unviable, and wasps that develop in them suffer negative fitness consequences. Egg stacking is more when parasitoids are present (Deas and Hunter, 2011).

4.2 Competition

4.2.1 Oviposition site shifting

Adult predatory coccinellid beetle *Coccinella septempunctata* are retained in a habitat if sufficient food resources are present. The abundance and quality of food in a habitat affects the reproductive output of a female and survival of larvae. Coccinellids increase reproduction in response to non-prey foods, but avoid ovipositing in areas with copious amount of honeydew. These coccinellids exhibit sibling cannibalism, so adult beetle avoid egg predation by reducing oviposition, where other adults are present, ovipositing on plants associated with less exposure or incidence of intraguild predation, and avoiding areas with tracks and frass of con- and heterospecific larvae (Seagraves, 2009).

4.2.2 Oviposition deterring pheromone

Insect parasitoids are known to deposit chemical signals on utilized hosts following oviposition. It is believed that these chemical signals alert future conspecifics of an exploited and thus sub-optimal host alleviating potential suffering among brood that would otherwise compete overa limited resource. *Diachasma alloeum* is a braconid wasp that specifically attacks two species of fruit-parasitic flies in the genus *Rhagoletis*. Female wasps lay a single egg into a second or third instar fly maggot developing in blueberry, hawthorn, or apple fruit. Following oviposition, female wasps press and drag their ovipositor across the fruit surface depositing a clear liquid; this has been termed 'excreting' behaviour (Stelinski *et al*., 2007).

4.3 Resource availability

4.3.1 Flower abortion in *Yucca glauca*

Phytophagous insects use a wide range of indicators or associated cues to avoid laying eggs in sites where offspring survival is low. For insects that lay eggs in flowers, these unsuitable sites may be created by the host plant's resource allocation to flowers. In the sequentially flowering host plant, *Yucca glauca*, late- opening distal flowers are more likely to be aborted in the presence of already- initiated basal fruits because they are strong resource sinks. If flowers are aborted, all eggs of the phytophagous insect, *Tegeticula yuccasella*, within the flower die. *T. yuccasella* was significantly less likely to oviposit in distal flowers on inflorescences with basal fruits and arrival of moth was higher at inflorescences with larger floral display size and earlier in the flowering season (Jadeja and Tenhumberg, 2017). These findings uncover a novel indicator of unsuitable oviposition sites - the presence of basal fruits that phytophagous insects use to make oviposition decisions. Possible proximate cues for *T. yuccasella* to reject distal flowers with basal fruits as oviposition sites include tactile and/or chemical cues from fruits and/or flowers.

4.3.2 Interaction between Wire worm *Agriotes lineatus* and *Spodoptera littoralis*

Plant-induced responses elicited by root herbivores have been shown to affect feeding and development of aboveground herbivores. However, little is known about how root feeding affects host choice behaviour of aboveground herbivores, including both adult oviposition behaviour and larval host acceptance. Root feeding by the wireworm, *Agriotes lineatus*, influences oviposition decisions and larval leaving rate of an aboveground herbivore, *Spodoptera littoralis*. Female *S. littoralis* deposited more and larger egg batches on undamaged plants when compared with wireworm infested plants. In a larval feeding experiment, a higher percentage *S. littoralis* larvae moved away from the wireworm-infested plant onto a neighbouring undamaged plant as compared with larvae feeding on previously undamaged plants(Anderson *et al.*, 2011). Larvae did not show an increased tendency to leave when feeding on plants previously exposed to conspecific larvae. Indirect interactions between belowground and aboveground herbivores extend to behavioural avoidance, both in terms of oviposition and larval feeding decisions. This allows the foliar herbivore to avoid systemic plant responses elicited by root herbivory, which likely represent reduced food quality and increased apparency toward natural enemies.

4.4 Host defense

4.4.1 Defense mechanism in black scale *Saissetia oleae*

Black scale *Saissetia oleae* having two forms of defence mechanism. One is due to hard integument and another case protection by ants. Argentine ant *Linepithema humile* is always in association with this black scale. *Metaphycus anneckei, M. hageni* and *M. lounsburyi* are the three encyrtidparasitoids of black scale. *M. anneckei* oviposit on soft ventral integument *M. hageni* and *M. lounsburyi* oviposit on harder dorsal integument. *Metaphycus anneckei* will oviposit success fully in the presence of ants because the host handling time less compared to others. But in case of other two species parasitism is less (Marco and Kent, 2001).

Table 6. Host handling and host feeding time of *Metaphycus* spp.

Parasitoid	**Host handling (seconds)**			**Host feeding**
	Host acceptance	Host rejection	Drilling and oviposition	
M. anneckei	**12.1[a]**	**6.9[a]**	**28.1[a]**	**-**
M. Hageni	19.9[b]	14.0[b]	179.7[b]	774
M. lounsburyi	28.0[b]	20.1[b]	178.3[b]	874

4.5 Tritrophic interaction

4.5.1 Host plant - prey - natural enemy

Tritrohic interaction between Host plant- preys - natural enemy. Hover fly *Episyrphus balteatus* larvae are a predator of aphids. Hover fly will not lay eggs on the plant were sinigrin content is more. Amiri-Jami *et al*. (2016) studied in two aphids *Brevicornye brassicae* it is a specialist prey and *Myzus persicae* is a generalist prey and host plant and *Brassica nigra* having high amount of sinigrin. They examined the oviposition preference of hoverfly towards oviposition site quality. *Brevicornye brassicae* have the ability to sequester the sinigrin content in plant into their body but not in *Myzus persicae.* Eggs are laid by female hover fly is more on *Myzus persicae* than other aphid.

Fig 5. Sinigrin content *B. brassicae* and *M. persicae* reared on *B. nigra*

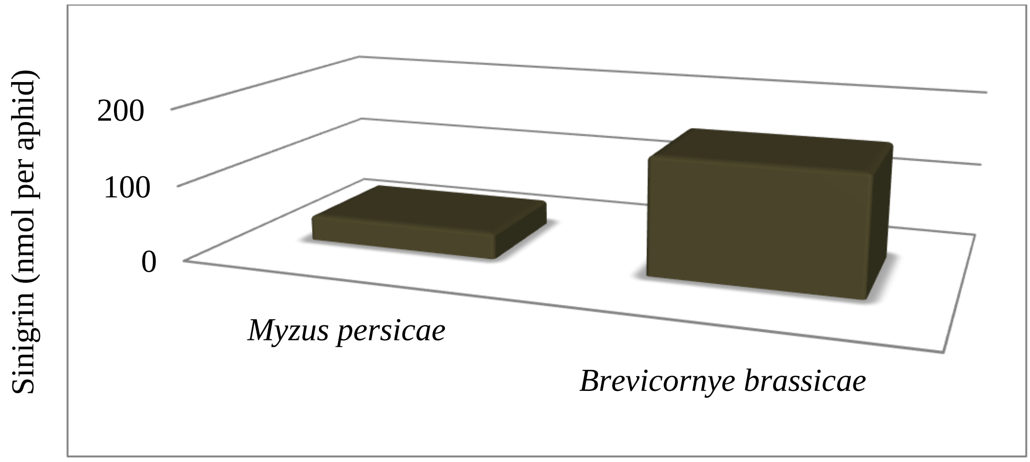
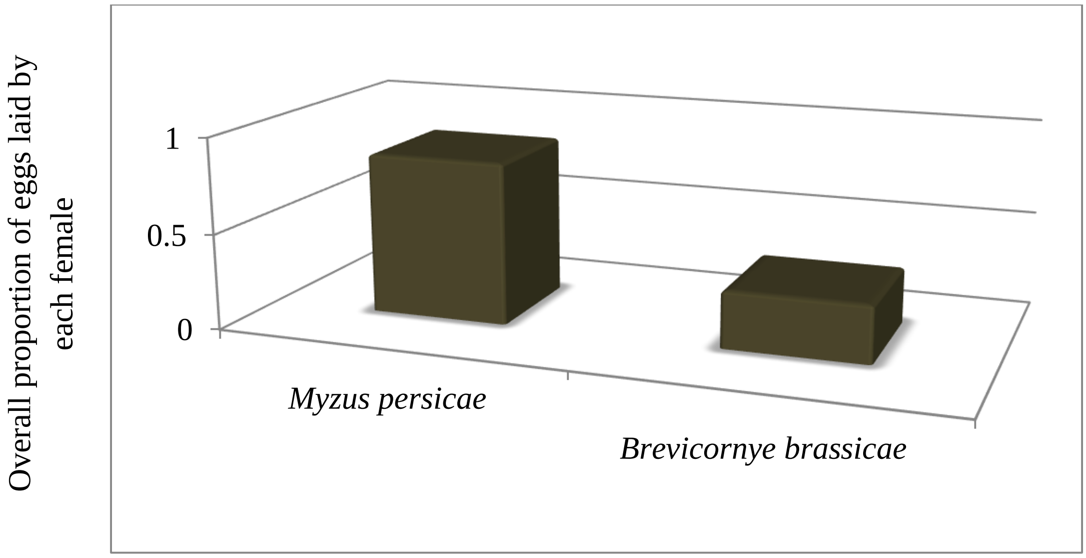


Fig 5. Eggs laid by female *Episyrphus balteatus* on aphid



5. Conclusion

The decisions made by mother insects on where to lay her eggs have influence on survival, growth, and reproductive potential of the offspring. Hence oviposition site selection is critical in deciding the host range of a species. The life cycle of most insect herbivores is closely associated with one or a few host plants .This ubiquitous specialization stimulated the development of several hypotheses on how natural selection should shape feeding and oviposition preferences of insect herbivores.

Larval stages usually have limited mobility, feeding on the host plants selected by their mothers. It is expected that natural selection will favour females that are able to discriminate among potential hosts and oviposit on plants that will increase offspring's survival. When larvae and adults feed on the leaf tissue of more than one host plant, it is possible that hosts that maximize offspring's growth and survival are not the same host plants that increase adult longevity. This situation can generate parent-offspringconflicts. In such cases, female fitness can be maximized in two different ways. Females may prefer to oviposit on the host plants that increase offspring survival, as predicted by the "mother knows best" principle. An alternative is that adults will spend more time feeding and laying eggs on the host plant that increases their own longevity, even if the consequence of this behavior is a reduction of offspring survival. Such scenario is known as the "optimal bad motherhood" principle.

6. Discussion

1. What you mean by HIPVs and its example?

HIPVs (Herbivore Induced Plant Volatiles) are released from leaves, flowers, and fruits into the atmosphere or into the soil from roots in response to herbivore attack. These chemicals used by the parasitic insects to find their host for oviposition.
Eg: After the attack of *Spodoptera exigua*in maize, plant release a terpene compound and attracted by several parasitoids for their oviposition into *Spodoptera exigua*.

2. What is the significance for studying insect oviposition behaviour?

Weed goldenrod *Solidago altissima* biological control programs using herbivorous insect as agents *Corythucha marmorata*, this is an outbreak species. Females of outbreak species tend to lay their eggs in batches as opposed to scattering their eggs throughout a stand of the host plant. In some extreme cases, the females are flightless and deposit all their eggs in a single mass. Often the larvae feed in groups, sometimes constructing webs or other sorts of group shelters.

3. Why green lacewings lay eggs as pedicellate type?

It is mainly for avoiding predation by ants. They will walk on the leaves so at that time avoid direct contact with eggs

4. The decisions made by mother on where to lay her eggs is critical for the survival, growth and reproductive potential of the offspring, so it is like that in all cases?

Not in all cases, but one meta-analysis study reported that about 75 per cent of insect follows mother knows best hypothesis than another hypothesis. So mainly mother will decide a place for oviposition not only for their own longevity but also for offspring survival.

5. Is there any example regarding optimal bad motherhood hypothesis?

Yes. Adult performance and oviposition preference of *Chromatomyia nigra* in four different grass species. It was found that the offspring survival and pupal size more or the grass *Lolium perenne* and but the adult showed more performance towards the grass species *Poa trivialis* as well as more number of eggs and feeding punctures more in this grass. Here female prefer to oviposit on the plant that maximize her fitness. Hence in this adult performance determine the host choice.

7. Reference

Aldrich, J. R., Khrimian, A., Zhang, A., and Shearer, P. W. 2006. Bug pheromones (Hemiptera, Heteroptera) and tachinid fly host-finding. *Museum*. Available: https://naldc.nal.usda.gov/download/17381/PDF [Accessed 20 October 2019].

Amiri-Jami, A. R., Sadeghi, H., Gilbert, F., Moravvej, G., and Asoodeh, A. 2016. Oviposition preference of aphidophagous hoverflies toward oviposition site quality: The presence of intra-and interspecific competitor, glucosinolate content, and prey species. *J. Asia pac. Entomol.* 19(2): 275-280.

Anderson, P., Sadek, M. M., and Wäckers, F. L. 2011. Root herbivory affects oviposition and feeding behavior of a foliar herbivore. *Behav. Ecol.* 22(6): 1272-1277.

Angelon, K. A. and Petranka, J. W. 2002. Chemicals of predatory mosquito fish (*Gambusia affinis*) influence selection of oviposition site by *Culex* mosquitoes. *J. chem. Ecol.* 28(4): 797-806.

Bernath, B., Szedenics, G., Wildermuth, H., and Horvath, G. 2002. How can dragonflies discern bright and dark waters from a distance? The degree of polarisation of reflected light as a possible cue for dragonfly habitat selection. *Freshw. Biol.* 47(9): 1707-1719.

Deas, J. B. and Hunter, M. S. 2011. Mothers modify eggs into shields to protect offspring from parasitism. *Proc. R. Soc. B: Biol. Sci.* 279(1730): 847-853.

García- Robledo, C. and Horvitz, C. C. 2012. Parent–offspring conflicts, "optimal bad motherhood" and the "mother knows best" principles in insect herbivores colonizing novel host plants. *Ecol. Evol.* 2(7): 1446-1457.

Gullan, P. J. and Cranston, P. S. 1994. *The insects: An Outline of Entomology*. John Wiley & Sons Ltd., UK, 595p.

Jadeja, S. and Tenhumberg, B. 2017. Phytophagous insect oviposition shifts in response to probability of flower abortion owing to the presence of basal fruits. *Ecol. Evol.* 7(21): 8770-8779.

Lopez-Ortega, M. and Williams, T. 2018. Natural enemy defense, provisioning and oviposition site selection as maternal strategies to enhance offspring survival in a sub-social bug. *PLOS ONE* 13(4): e0195665. Available: https://doi.org/ 10.1371/journal.pone.0195665 [Accessed 20 October 2019].

Marco S, B. and Kent M, D. 2001. Host- handling behaviours in parasitoids of the black scale: a case for ant- mediated evolution. *J. Anim. Ecol.* 70(2): 237-247.

Mayhew, P. J. 1997. Adaptive patterns of host - plant selection by phytophagous insects. *Oikos* 79: 417-428.

Messing, R. H., Klungness, L. M., Jang, E. B., and Nishijima, K. A. 1996. Response of the melon fly parasitoid *Pysttalia fletcheri* (Hymenoptera: Braconidae) to host-habitat stimuli. *J. Insect Behav.* 9(6): 933-945.

Obonyo, M., Schulthess, F., Van den berg, J. O. H. N. N. I. E., and Calatayud, P. A. 2010. Host recognition and acceptance behaviour in *Cotesia sesamiae* and *C. flavipes* (Hymenoptera: Braconidae), parasitoids of gramineous stemborers in Africa. Eur. J. Entomol. 107: 169-176 ·

Ozaki, K., Ryuda, M., Yamada, A., Utoguchi, A., Ishimoto, H., Cala, D., Marion-Poll, F., Tanimura, T., and Yoshikawa, H. 2011. A gustatory receptor involved in host plant selection for oviposition of a swallow tail butterfly. *Nat. Commun.* 2: 542.

Scheirs, J., Bruyn, L. D., and Verhagen, R. 2000. Optimization of adult performance determines host choice in a grass miner. *Proc. R. Soc. Lond. Ser. B: Biol. Sci.* 267(1457): 2065-2069.

Seagraves, M. P. 2009. Lady beetle oviposition behavior in response to the trophic environment. *Biol. Control* 51(2): 313-322.

Steidle, J. L. 2000. Host recognition cues of the granary weevil parasitoid *Lariophagus distinguendus*. *Entomologia Experimentaliset Applicata* 95(2): 185-192.

Stelinski, L. L., Oakleaf, R., and Rodriguez-Saona, C. 2007. Oviposition-deterring pheromone deposited on blueberry fruit by the parasitic wasp, *Diachasma alloeum*. *Behaviour* 144(4): 429-446.

Thrasher, P., Reyes, E., and Klug, H. 2015. Parental care and mate choice in the giant water bug *Belostoma lutarium*. *Ethology* 121(10): 1018-1029.

Walker, T. J. 1993. Phonotaxis in female *Ormia ochracea* (Diptera: Tachinidae), a parasitoid of field crickets. *J. insect behav.* 6(3): 389-410.

8. Abstract

KERALA AGRICULTURAL UNIVERSITY

COLLEGE OF HORTICULTURE, VELLANIKKARA

Department of Agricultural Entomology

ENT 591: Master's Seminar

Name	: Beegam Salma M.P.	Venue	: Seminar Hall
Admission no.	: 2018-11-117	Date	: 15-11-2019

Major Advisor: Dr.Vidya C.V.   Time : 10:45 am

Mother knows best: oviposition behaviour in insects

Abstract

Oviposition is the process by which egg passes from the external genital opening or vulva of the female insect to the outside (Gullan and Cranston, 1994). Insects oviposit either directly through gonopore, which is present behind the eighth or ninth abdominal segment or through a specialised structure called ovipositor. Insects such as butterflies, moths and beetles lay eggs directly through gonopore, whereas grasshoppers, crickets and many parasitic wasps lay eggs using ovipositor.

Oviposition preferences due to natural selection result in specialization of insect herbivores to one or a few host plants. The oviposition preference of mother is explained by two hypotheses: mother knows best hypothesis and optimal bad motherhood hypothesis. The 'mother knows best hypothesis' suggests that females prefer to oviposit on hosts that increase offspring survival. According to this hypothesis, host preference pattern is shaped by offspring performance (Mayhew, 1997). The 'optimal bad motherhood hypothesis' predicts that females prefer to oviposit on hosts that increases their own longevity. Here, host preference pattern is shaped by adult performance (Scheirs *et al*., 2000).

Behavioural events leading to oviposition are based on stimuli that elicit a response in insects. The sequence of events in host selection for oviposition by an adult female include host habitat finding, host finding, host recognition and finally host acceptance. Host habitat finding is an orientation process, where the insect utilizes mainly visual and chemical stimuli. Dragonflies, *Aeshna juncea* and *Orthetrum brunneum* use polarization of reflected light as stimuli for identifying the host habitat (Bernath *et al.*, 2002).

Host finding is the final step in orientation, where insects respond to visual, chemical and acoustic stimuli from the host. Many insects cannot recognise their host from a distance, but can distinguish by contact evaluation, which is referred to as host recognition. Butterflies recognise their host by drumming with tarsal segments, tapping with antennae and probing with proboscis. The swallow tail butterfly, *Papilio xuthus* uses chemosensilla present on the fifth tarsomere of forelegs for recognizing the oviposition stimulant, synephrine, in its host plant. The gustatory receptor gene, *PxutGr1*recognizes synephrine from the host plant (Ozaki *et al*., 2011). The final event in host selection is oviposition, which indicates host acceptance.

There are many challenges encountered by the mother insect that decide or modify its oviposition behaviour. Major challenges are predation risk, competition, resource availability, host defence and tritrophic effect. The strategies adopted by females to overcome these challenges are oviposition avoidance, oviposition site shifting, reducing the host handling time and protection of eggs. The pentatomid bug, *Ramosiana insignis* shifts its oviposition site to non-host plants which reduce the risk of parasitism (Lopez-Ortega and Williams, 2018).

The decisions made by mother on where to lay her eggs is critical for the survival, growth and reproductive potential of the offspring.

References

Bernath, B., Szedenics, G., Wildermuth, H., and Horvath, G. 2002. How can dragonflies discern bright and dark waters from a distance? The degree of polarisation of reflected light as a possible cue for dragonfly habitat selection. *Freshw. Biol.* 47(9): 1707-1719.

Gullan, P. J. and Cranston, P. S. 1994. *The insects: An Outline of Entomology*. John Wiley & Sons Ltd., UK, 595p.

Lopez-Ortega, M. and Williams, T. 2018. Natural enemy defense, provisioning and oviposition site selection as maternal strategies toenhance offspring survival in a sub-social bug. *PLOS ONE* 13(4): e0195665. Available: https://doi.org/ 10.1371/journal.pone.0195665 [Accessed 20 October 2019].

Mayhew, P. J. 1997. Adaptive patterns of host - plant selection by phytophagous insects. *Oikos* 79: 417-428.

Ozaki, K., Ryuda, M., Yamada, A., Utoguchi, A., Ishimoto, H., Cala, D., Marion-Poll, F., Tanimura, T., and Yoshikawa, H. 2011. A gustatory receptor involved in host plant selection for oviposition of a swallow tail butterfly. *Nat. Commun.* 2: 542.

Scheirs, J., Bruyn, L. D., and Verhagen, R. 2000. Optimization of adult performance determines host choice in a grass miner. *Proc. R. Soc. Lond. Ser. B: Biol. Sci.* 267(1457): 2065-2069.