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Popular Article

Adaptive Plasticity of Insect Eggs in Response to Environmental Challenges

Srikantha J K, Arunakumar Muli, Naveenkumar K, Shubha J K

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Introduction

All organisms adjust their development and physiology when confronted with environmental changes to ensure that they can produce the functional structures necessary for survival and reproduction. While some traits are remarkably invariant across environmental changes, others show high degrees of variation, known as plasticity. This plasticity is found on all the living organisms and the ability of an organism to modify its phenotype or behaviour in response to changing environmental conditions to increase its chances of survival and reproduction is known as “adaptive plasticity “.

Most insect species are oviparous and expose their eggs to many environmental changes. Despite plethora of factors that endanger eggs, oviparity is obviously a successful strategy, which is due to innate developmental program and genetically determined protective traits provided by the parents. In addition, there is increasing evidence that parents adjust the egg phenotype to the actual needs, eggs themselves respond to environmental challenges, and egg-associated microbes actively shape the egg immunity. Being a sessile stage insect egg gains attention by interacting with its environment which is two way. The major factors threatening the insect eggs are, abiotic factors-temperature, ultra violet rays (UV), moisture and biotic factors include pathogens, predators and parasitoids.

1. PLASTICITY IN RESPONSE TO ABIOTIC CONDITIONS

1.1.1 Thermal plasticity

Thermal stress in insect egg affects the metabolism and survivality. Thermal stress is felt at cellular and biochemical level. This will causes the proteins to unfold which causes the aggregation of proteins and finally become toxic. Mobile insects may easily escape from this but being sessile stage insect egg may be overcome by (a) Their parents, (b) by own and (c) by parent micro biome.

1.1.2 Thermal plasticity contributed by mother

Insect mothers contribute to thermo protection of their eggs by several means. The maternal timing of egg deposition and the choice of oviposition sites significantly contribute to egg survival. Furthermore, covering 4 eggs with plant tissue, feces, or maternal secretions can protect overwintering offspring from detrimental temperatures. In addition to such protective measures, insect mothers endow the inside of their eggs with maternal messenger RNA, proteins, lipids, and carbohydrates, which provide the initial developmental basis for the embryo. In the very early embryonic stage, this maternal provisioning of the eggs contributes to thermo protection via compounds such as heat shock proteins or cryoprotective lipids.

To confirm the contribution of mother in thermo protection of its egg, Lockwood et al. (2017) studied the mRNA level of the heat shock proteins (HSPs) in Drosophila parents, embryo and 4 day old heat shocked adult and concluded that among all the HSPs, HSP23 have shown the difference in between embryo and the heat shocked adult. Whereas, mRNA level of HSP23 in normal adult is low. Further, to know the effect of this in thermal tolerant of the offsprings they over expressed the HSP23 in the mother by using certain systems. They compared the HSP23 mRNA level in offsprings obtained by the mother having over expressed genes and from normal mother at two different temperature 22 0C and 30 0C. Then observed that mRNA level of the offsprings obtained by over expressed mother was having higher mRNA level when compared to normal offspring at both temperature. They further analysed the hatching, pupation and eclosion percentage where, they found that there is 1 0C rise in lethal temperature. Finally they concluded that single genes of large effect can contribute significantly to whole organism phenotypes, such as thermal tolerance and that maternal loading of mRNAs can influence not only early embryonic development but also larval performance later in life.

1.1.3 Thermal plasticity by own:

Youngjin and Yonggyun (2013) conducted a study witnessing the temperature experienced by the egg shown to have effect on their thermal resistance in Beet armyworm Spodoptera exigua. Though hit was sensitive to frost, very problematic in the temperate zone only. This behaviour is due to their supercooling habit. To survive in cold temperature without going to diapauses they expose themselves to low temperature so that they can survive still survive better in upcoming very low temperature. This was experimentally proven by the scientists transferring the S. exigua eggs at 4 0C before transferring to -10 0C and compared the survivality percentage of these eggs with eggs that have transferred directly at -10 0C and they found that the glycerol is the rapid cold hardening factor here

1.1.4 Thermal plasticity Parental microbiome:

In addition to parental and zygotic influences, the parental microbiome plays a key role in the thermotolerance of insect eggs. The microbiome composition changes with temperature and affects the offspring's gene expression response to temperature. While how insect eggs sense temperature is still unclear, thermosensitive proteins like TRP channels (especially TRPA1) are involved. These are expressed in insect eggs and may help regulate diapause. In *Bombyx mori*, warm temperatures trigger TRPA1, leading to diapause hormone (DH) production during pupal stages, causing females to lay diapausing eggs. However, the exact signaling pathway for this intergenerational diapause regulation remains unknown

1.2 Egg Responses to Drought

Protection of insect eggs from desiccation, like thermal protection, is strongly influenced by maternal oviposition behavior, including the selection of egg-laying sites and clustering of eggs. Mothers may also enhance egg resistance to drying by supplying them with internal water, enriching the eggshell with hydrocarbons, or coating them with protective substances such as hydrogels. For instance, mosquitoes lay their eggs in water collections, some of which are temporary. During early embryogenesis, eggs are vulnerable to dehydration. However, the development of the serosal cuticle, a protective layer surrounding the embryo, enhances their ability to survive outside water. The desiccation resistance among mosquito genera varies: *Aedes* eggs can survive the longest, followed by *Anopheles* and then *Culex*. Farnesi et al. (2017) found that this variation is linked to the level of eggshell melanization, with darker eggs showing greater resistance to water loss. This protective effect depends on the proper formation of both melanin and the serosal cuticle, as confirmed using mutants deficient in melanization. The serosa and its cuticle play a key role in drought resistance, which may be further strengthened by the presence of dark eumelanin in the endochorion. Accelerated formation of these protective layers under low humidity conditions may benefit egg survival, although it remains unclear whether developmental timing can be actively adjusted to environmental conditions. Additionally, it is not yet known whether insect eggs can regulate their physiological water needs beyond programmed developmental traits. Future research should focus on understanding how eggs maintain internal water balance—possibly through mechanisms such as modifying eggshell conductance, actively absorbing water vapor, or passively absorbing water via osmotic forces.

1. 3 Exposure to UV light

Exposure to UV light results in generation of reactive oxygen species (ROS), which have the potential to cause cellular damage. Pigmentation by melanin can protect the egg from damage by UV light. Melanin is highly efficient in adsorbing especially the short wavelengths of solar light via its numerous cyclic structures with conjugated electron pairs. While melanization of the egg shell is part of the innate developmental program in some insects, females of the stink bug *Podisus maculiventris* can adjust coloration of their eggs by melanin to the expected exposure to UV light. Even in the absence of melanin, the egg shell can provide protection from damage by UV light, it has been found for *Manduca sexta* eggs, which are colored greenish by yellow carotenoids and a blue biliprotein, insecticyanin. Carotenoids are very common egg pigments, and they also are expected to contribute to protection of eggs from UV radiation damage due to their ROS scavenging properties.

2. INSECT EGG DEFENSES AGAINST BIOTIC THREATS

As sessile life stages, insect eggs are exposed to a high risk of parasitization and predation. They are a protein-rich food source not only for parasitoids and many predatory insects, but also for other arthropods like spiders and even for birds. Infection of eggs by pathogenic bacteria is uncommon but may occur, for example, via maternal transfer of bacteria to the oocyte or via attack by parasitoids. Infection of eggs by fungi, which can penetrate the egg shell with their hyphae, is more widespread than bacterial disease of eggs.

a. Constitutive defensive responses of eggs to pathogens and parasitoid

Constitutive egg defences are provided by parents in numerous ways. Females of Many insect species incorporate defensive compounds into their oocytes or into secretions Deposited with the eggs. These compounds are either produced de novo or sequestered from Food. In addition, symbiotic microbes harbored by the mother are known to produce Defensive compounds contributing to egg protection. Insect fathers can contribute to Protection of eggs from biotic threats by transferring defensive chemicals to females during Mating. The females incorporate these compounds into the eggs or into secretions coating the Eggs. Alternatively, some insects protect their eggs with sticky fecal covers or hairy tufts that Impair access to the eggs or provide parental brood care by guarding, carrying, or grooming Egg.

Insects employ various constitutive egg defenses, often provided by the parents. Many insect females incorporate defensive compounds into their oocytes or into secretions that accompany the eggs. These compounds may be synthesized by the mother or obtained from her diet. Additionally, symbiotic microbes residing in the mother can produce protective substances that enhance egg defense. Male insects can also contribute by transferring defensive chemicals to females during mating, which are then deposited into or onto the eggs. In some species, eggs are protected with sticky fecal coatings or hairy tufts that deter predators or parasitoids by making the eggs less accessible. Some insects also exhibit parental care, such as guarding, carrying, or grooming their eggs, to enhance their survival.

So far, there is no definitive evidence that insect parents adjust the level of defensive compounds provided to their eggs based on the actual risk of predation. However, they may respond to predation threats by modifying their oviposition behavior, such as choosing egg-laying sites with fewer predators, thereby reducing the likelihood of egg predation. In addition to parental contributions, eggs themselves produce constitutive defenses against microbial infections, even in the absence of biotic threats. These include immune-related proteins and antimicrobial peptides. For instance, freshly laid, unchallenged eggs of *Manduca sexta* constitutively express immune genes that code for prophenoloxidase activating protease (PAP I), prophenoloxidase (ProPO), and various antimicrobial peptides. Similarly, in *Tribolium confusum* beetles, the serosa—a protective extraembryonic membrane—shows constitutive expression of immune genes encoding microbial recognition receptors, proteins from the Toll and IMD signaling pathways, and class B scavenger receptors. These findings support the role of the serosa as an immune-competent barrier that protects the developing embryo.

The constitutive production of low molecular weight defensive compounds by insect eggs is rare. However, a remarkable exception is found in the European beewolf (*Philanthus triangulum*), whose eggs emit nitric oxide (NO) radicals. These eggs are laid in underground brood cells, where they face a high risk of microbial infection. The nitric oxide released reacts with oxygen to form nitrogen dioxide (NO_2) radicals, which possess strong antifungal properties when produced in sufficient quantities. This unique defense mechanism is believed to result from a special modification of nitric oxide synthase (NOS)—an enzyme commonly involved in cellular regulation across many organisms. In the beewolf, this enzymatic modification likely represents a key evolutionary adaptation that enables the eggs to generate high levels of nitric oxide for microbial defense.

Symbiont-mediated protection is increasingly recognized as a common form of constitutive egg defense, particularly in insect species that lay eggs in environments with high pathogen risk. Fungal and bacterial symbionts, transmitted either to the oviposition site or directly onto the eggs, help protect them from infection and predation. Symbiont-containing secretions not only ensure the transfer of essential microbes but may also support early larval development by providing nourishment. This section highlights the protective role of microbes released during oviposition.

Many species of ants, termites, and beetles are known to transport fungal spores to their oviposition sites as part of a strategy to grow fungal gardens. These gardens serve as both a nutritional source and a form of protection for their developing offspring. In termite nests, for instance, fungal mycelia not only support larval growth but also produce various secondary metabolites, including compounds with antimicrobial properties, thereby contributing to egg and larval protection from microbial threats.

This method of provisioning and protecting offspring through fungiculture is well documented in social insects like termites, but it is also found in some non-social insect clades. A notable example is the weevil *Eups chinensis*, which engages in leaf rolling to create protective plant "cradles" for its eggs. These cradles are inoculated with spores of *Penicillium herquei*, a symbiotic fungus that the female weevil carries in specialized organs called mycangia, designed specifically for transporting fungi. Within a few days, the fungal mycelium grows to encase the eggs, providing a dual function: it serves as food for the hatching larvae and offers protection from harmful microbes.

The fungus *P. herquei* not only supports nutrition but also suppresses the growth of competing plant-associated bacteria, fungi, and pathogens. Biochemical studies have identified that *P. herquei* produces (+)-scleroderolide, a broad-spectrum antimicrobial compound that confirms the fungus's role in egg defense.

Insect species that oviposit in microbially rich environments—such as the house fly (*Musca domestica*), which lays eggs in animal manure—employ a different but similarly effective strategy. Female house flies coat their eggs with a bacterial consortium composed of multiple species. This microbial coating helps suppress pathogenic fungi, ensuring that the nutrient-rich but microbially hazardous environment does not threaten egg viability. Interestingly, the inhibitory effects of this bacterial community are synergistic, with protection likely resulting from both chemical antimicrobial activity and competitive exclusion of harmful microbes.

An emerging area of research highlights the importance of horizontal gene transfer (HGT) in enhancing the defensive capabilities of microbial symbionts. HGT allows bacteria to acquire genes encoding secondary metabolites and toxins, as demonstrated in symbiotic microbes of aphids, psyllids, beetles, and even marine sponges. A striking example involves Pseudomonas bacteria symbiotically associated with rove beetles (Staphylinidae), particularly those in the genus *Paederus*. These bacteria produce pederin, a highly toxic polyketide compound, which provides chemical defense against predators. Notably, eggs and larvae of *Paederus* species show higher concentrations of pederin than later life stages, reflecting the increased vulnerability of immature stages to predation.

The genes responsible for pederin biosynthesis appear to have been acquired by Pseudomonas through horizontal gene transfer, which is supported by the genetic homology observed between the pederin gene cluster and similar gene clusters in unrelated symbionts, such as those producing diaphorin in psyllids. This suggests that HGT is a widespread evolutionary mechanism enabling microbial symbionts to evolve protective traits that benefit their insect hosts, especially during early life stages.

3. Induced defensive responses of eggs to pathogens and parasitoids

Insect eggs are not passive targets during pathogen infections or parasitoid attacks; instead, they actively mount immune responses that are similar to those observed in larvae, pupae, and adults. Upon infection, the immune reaction is triggered not only in the embryo itself but also in the extraembryonic tissue, particularly the serosa, which often plays a crucial role in defending the developing embryo.

When pathogens invade, eggs initiate cellular immune responses, which include processes such as phagocytosis—where immune cells engulf and digest foreign particles—and encapsulation, in which the invading organism is surrounded and isolated by immune cells. In addition to these cellular responses, eggs also exhibit humoral immune responses, which involve the production of antimicrobial peptides (AMPs) and the melanization of the invader. Melanization surrounds the pathogen with a melanin-rich barrier, effectively immobilizing and neutralizing it. These immune defenses are largely mediated by embryonic hemocytes, the immune cells present in the developing embryo.

The role of the serosa—a protective extraembryonic membrane—varies between species but can be vital in mounting immune responses in some insects. For example, in the cerambycid beetle *Phoracantha recurva*, the eggs respond to parasitism by the encyrtid wasp *Avetianella longoi* through a strong immune response. The parasitoid egg and larva are subjected to cellular encapsulation and melanization, which significantly increases the survival rate of the beetle eggs by effectively neutralizing the parasitoid.

In contrast, the eggs of the tobacco hornworm (*Manduca sexta*) do not survive parasitism despite initiating an immune response. When parasitized, *M. sexta* eggs exhibit upregulation of several immune-related genes, indicating a molecular attempt to fight back. However, this response is insufficient to prevent egg mortality. Still, it does lead to a notable decrease in the survival rate of the parasitoid, suggesting that even partial immune activation can impose a cost on the attacking organism.

In summary, insect eggs possess active immune capabilities involving both cellular and humoral mechanisms, and while the effectiveness of these responses varies across species, they play a crucial role in enhancing egg survival under biotic stress conditions.

4. INSECT EGGS IN DYNAMIC INTERACTION WITH THEIR ENVIRONMENT

4.1. Oviposition by herbivores affects the plant:

Eggs laid by herbivorous insects can trigger defensive responses in plants that are specifically directed against the insect eggs themselves. These plant responses are not passive; rather, they are active defense mechanisms that include the induction of localized tissue damage, such as a hypersensitive response (HR)-like leaf necrosis, or the formation of neoplasms, which are abnormal tissue growths. These structures may lead to the desiccation of the insect eggs or cause the eggs to detach from the plant surface, thereby preventing further damage from developing larvae.

In addition to these physical responses, plants can also produce ovicidal (egg-killing) compounds in response to egg deposition. Another sophisticated strategy employed by plants is the emission of volatile organic compounds (VOCs) after insect eggs are laid. These volatiles serve as chemical signals that attract egg parasitoids, which are natural enemies of insect eggs. The parasitoids use these volatiles to locate the eggs and parasitize or kill them, thereby providing an indirect but highly effective means of plant defense.

Recent research has increasingly focused on the molecular and physiological mechanisms that underlie these plant responses to insect eggs. Interestingly, the plant responses to insect eggs show striking similarities to the responses activated during plant-pathogen interactions. For example, when plants detect the presence of insect eggs, they often exhibit HR-like necrosis, accumulation of reactive oxygen species (ROS), and increased levels of salicylic acid (SA)—a key hormone involved in plant defense signaling. These changes are accompanied by the upregulation of SA-responsive genes, including pathogenesis-related (PR) genes, which are typically activated during immune responses to microbial pathogens. Furthermore, plants also accumulate phenylpropanoid compounds, which contribute to structural and chemical defenses.

These findings suggest that insect eggs can act as elicitors that activate plant immunity in ways that are both specific to the insect threat and similar to the responses used against microbial pathogens. This dual utility is particularly beneficial in nature, as insect oviposition can potentially introduce phytopathogens into plant tissues, making the early detection and response to eggs an important component of plant health and survival.

Moreover, plant responses to insect eggs can be primed or enhanced by prior exposure to insect-derived chemical cues. A notable example is the interaction between Pinus sylvestris (Scots pine) and the herbivorous sawfly *Diprion pini*. Research has shown that when pine trees are exposed to the sex pheromones of *D. pini* before egg laying occurs, they exhibit enhanced defensive responses against the eggs. This priming effect results in increased accumulation of hydrogen peroxide—a ROS involved in plant defense—and changes in gene expression profiles that improve the plant's ability to resist egg survival. Eggs laid on pheromone-exposed pine trees showed significantly lower survival rates than those on unexposed trees.

While these results demonstrate a powerful example of plant defense priming, the species specificity of such priming—whether it applies broadly or only to specific insect-host combinations—remains an area for future investigation. Nonetheless, these findings underscore the dynamic and highly adaptive nature of plant-insect interactions, particularly at the earliest stages of herbivore attack.

4.2. Oviposition affects further oviposition by second and third trophic level members:

Female herbivorous insects and parasitoids selecting oviposition sites can be either attracted or deterred by the presence of eggs from the same (conspecific) or different (heterospecific) species. Their decision may be influenced by chemical cues from already laid eggs or by plant responses triggered by oviposition. When herbivorous insects lay eggs on leaves, the plant responds by releasing oviposition-induced plant volatiles (OIPVs). These volatiles influence the behavior of other female herbivores and play a role in their oviposition choices.

OIPVs can function as signals of potential competition, warning that the plant already hosts eggs, and therefore may soon support developing larvae that will compete for resources. As a result, these volatiles may deter further egg-laying by other females. In contrast, egg parasitoids are often attracted to OIPVs, which guide them to the egg-laden plants. In some cases, parasitoids also respond to chemical changes on the leaf surface caused by egg deposition, increasing their host-searching activity.

The effects of OIPVs are not restricted to the egg-laden plant alone. In the case of the moth *Micromelalopha sieversi*, eggs laid on poplar leaves stimulated the emission of specific monoterpenes—3-carene and β-pinene—not only from the plant where the eggs were laid but also from neighboring plants. This plant-to-plant signaling reduced the number of eggs laid on nearby plants, indicating that volatiles can mediate community-level oviposition behavior.

In addition to OIPVs, oviposition-deterring pheromones (ODPs), which are chemical signals deposited by egg-laying females, can discourage other females from using the same site. These pheromones, either applied directly on the eggs or around the oviposition site, signal the risk of overcrowding and competition for limited resources. Although ODPs have known ecological effects, the specific chemical identities of these pheromones in herbivorous insects remain poorly characterized.

Similarly, parasitoid wasps use host-marking pheromones to signal that a host has already been used for oviposition. This allows other females to avoid depositing eggs in the same host, thereby preventing intraspecific competition between their offspring. The marking also benefits the marking female, especially when host resources are scarce, by preserving exclusive access to that host for her progeny.

However, in some scenarios, depositing multiple parasitoid eggs in one host may be beneficial. This strategy can overwhelm the host's immune system, such as encapsulation, increasing the chances of successful development for at least some of the parasitoid larvae. Thus, chemical communication via volatiles and pheromones plays a central role in shaping insect oviposition strategies, affecting both competition and survival outcomes.

4.3. Oviposition by parasitoids affects second and first trophic level members:

Oviposition into hosts is associated with an intriguing type of mutualism between the parasitoid host egg and certain types of viruses, so-called polydnaviruses (PDVs). The PDVs injected into host larvae by an egg-laying parasitoid not only inhibit encapsulation of parasitoid eggs and/or parasitoid larvae by the host’s immune system, but also lead to physiological changes in herbivorous host larvae. The viral infection reaches the salivary glands of the herbivorous host larvae, where viral-encoded proteins secreted with the host saliva into feeding sites may either directly change the host plant’s phenotype or manipulate the biosynthesis of plant defense elicitors in the host’s saliva. As a consequence, the plant’s defense against host larvae is attenuated, which may benefit the development of the parasitoid inside the host. However, hyperparasitoids are attracted by the odor of plants that are infested by parasitized, PDV-infected host larvae. Thus, parasitoid egg deposition associated with PDVs affects not only the second and first trophic levels, but also the fourth level.

CONCLUSIONS

While insect eggs have been intensively studied with respect to their innate developmental program, much less attention has been paid to their adaptive plasticity in response to environmental conditions. In addition to a plethora of parentally provided egg protective measures, the adaptive abilities of the insect eggs themselves must certainly have contributed to the evolutionary success of egg laying as a reproductive strategy in insects. However, we still do not really know how insect eggs sense their environment and how they sense temperature, relative humidity, and other crucial environmental information. 17 Furthermore, future studies need to address how events experienced in the egg stage affect later developmental stages. To date, egg-associated microbes have been shown to contribute to protection of eggs from biotic threats, but it remains to be explored whether egg-associated symbionts also contribute to protection from unfavorable abiotic conditions such as cold or drought. Moreover, it is now abundantly clear that insect eggs exert significant effects on various trophic levels, and these effects may cascade up and down in food webs. There is still a tremendous amount to be learned about the dynamic multipartite systems composed of host plants; parental insects and their eggs; and the plethora of parasitoids, predators, and pathogens that attack eggs.

References

Brakefield P M, Pijpe J and Zwaan B J, 2007, Developmental plasticity and acclimation both contribute to adaptive responses to alternating seasons of plenty and of stress in Bicyclus butterflies. *Journal of biosciences*, 32(1): 465-475.

Farnesi L C, Vargas H C, Valle D and Rezende G L, 2017, Darker eggs of mosquitoes resist more to dry conditions: Melanin enhances serosal cuticle contribution in egg resistance to desiccation in Aedes, Anopheles and Culex vectors. *PLoS neglected tropical diseases*, 11(10): 01 -20.

Harwood G, Amdam G and Freitak D, 2019, The role of vitellogenin in the transfer of immune elicitors from gut to hypopharyngeal glands in honey bees (Apis mellifera). *Journal of insect physiology*, 112(1): 90-100.

Hilker M, Salem H and Fatouros N E, 2023, Adaptive plasticity of insect eggs in response to environmental challenges. *Annual Review of Entomology,* 68(1): 451-469.

Lockwood B L, Julick C R and Montooth K L, 2017, Maternal loading of a small heat shock protein increases embryo thermal tolerance in Drosophila melanogaster. *Journal of Experimental Biology*, 220(23): 4492-4501.

Strohm E, Herzner G, Ruther J, Kaltenpoth M and Engl T, 2019, Nitric oxide radicals are emitted by wasp eggs to kill mold fungi. *Elife*, 8(1): 43718 - 43724.