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Study of nonreproductive effects of insect parasitoids

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Abstract

Parasitoids wasps are a natural enemy species that can be used in the biological control of pests, have many uses, and are a good model in theoretical ecology. The main purpose of the action of the parasitoids is to kill the host by oviposition and develop offspring, which eventually causes death due to reproduction of parasitoids. However, for some parasitoids species, the adult female may also feed from the host to obtain food for future reproduction of parasitoids, often resulting in the death of the host. The effect of parasitoids on the host is predictable if host deaths are excluded. After egg laying, both larvae and adults can cause the death of the host. The non-reproductive influence was established by Abram *et al.* (2019) in the absence of parasitoids or host. However, non-reproductive effects - May effects on the host, including death, but these are not beneficial to the parasitoids for immediate development. Different names have been used as, - *viz.*, failed parasitism, nonreproductive killing, hypersensitivity, dudding, host destruction, surplus killing, abortion, residual mortality, and parasitoids-induced other mortality. However, parasitoids can also adversely affect their hosts in ways that do not support the development of current or future offspring (other than fertility). Host conflict can adversely affect growth, behavior, reproduction, and mortality. In addition, Abram *et al.* (2019) divided non-reproductive effects into five groups, - (a) nonconsumptive effects; (b) mutilation; (c) pseudoparasitism; (d) immune defence expenses; and (e) aborted parasitism. A latent feature of the host-parasitoid trophic network is the non-reproductive phenomenon, which is useful for assessing the impact on communities as well as the ecosystem services provided by parasitoid for biological control.

Keywords: Parasitoids, biological control agents, reproductive parasitoid mortality, non-reproductive effects, parasitoid failure, Non-Reproductive Effect (NRE)

1. Introduction

The term "parasitoid" is coined by Sweden-Odonnish 1913. In general, parasitoids are insects that eat and grow larvae on or inside the body of other arthropods. But what makes the parasitoids special is its relationship with its host, and this comes at the expense of the host's life. Parasitism represents one of the six main mechanisms of change in parasitism resulting from the death of the host, similar to predation. Parasitoids can be divided into two classes, - idiobionts and koinobionts, which differ in their interactions with their hosts (Gullan *et al.*, 2010) ^[15]. The strategy used by idiobiont parasitoids is that they sting their larger prey soon after capture, causing them to death or be paralyzed instantly. The host is then moved to the nest, sometimes with other animals, if it is not large enough to support the development of parasitic disease. Eggs are laid on the prey and the nest is sealed. The parasitoid quickly passed on to development of offspring, eating all the bodily matter as food. In contrast, Koinobiont parasitoids, which include flies and wasps, lay their eggs on young hosts, which are usually larvae. These eggs continue to grow, allowing the host and parasitoid to coexist in the long run. When the parasitoid is matures and the animal is eaten from the inside, the process ends and dies. Some syncytials can control the development of the host, such as preventing parasitoids from pupating or causing molting when they are ready to molt. This change can be achieved by the production of hormones that stimulate the host's ecdysone (ecdysteroid) or directly affect the host's endocrine system. Insect parasitoids play an important role in the world's ecosystems and are widely used as biocontrol agents globally. They are also important models in ecological research (Godfray 1994 ^[13] & Heimpel & Mills, 2017 ^[17]). As a biocontrol agent, its main mode of action is to kill the host through egg laying and offspring development, *i.e.* Death through disease spread. In some parasitoid species, the adult female also feeds directly from the host to obtain nutrients for egg maturation, which often results in the death of the host (Jervis and Kidd, 1986^[19]). However, without good offspring or direct feeding, parasitoids can negatively affect their hosts (Abram *et al.*, 2019) ^[3]. These non-reproductive effects can have many adverse effects on the host, including death, but are not

beneficial for the parasitoid for current or future development (Abram *et al.*, 2019) [3]. However, Ahmed *et al.* (2016) [4] reported that the seasonal incidence of lepidopteran pest of cabbage is control by activity of parasitoid. Moreover, Saikia *et al.* (2017) [30] revealed the impact of *Cotesia* sp. on rice leaf folder. Parasitoid as an important component of biological pest control had a significant role in agri-horti ecosystem (Borkakati *et al.*, 2018) [8]; brinjal ecosystem (Saikia & Borkakati, 2019) [31]; mustard (Pradhan *et al.*, 2020) [28]; bhut jalakia (Buragohain *et al.* 2017a [10] and Buragohain *et al.* 2017b) [10, 11]. Parasitoid can use chemical or optical sense organ to find out their host (Borkakati *et al.*, 2019) [9]. Hence, there is an ample scope for popularizing the effect of parasitoid under Bio-Intensive Integrated Pest Management (BIPM) can be undertaken through different farmers friendly approaches of Krishi Vigyan Kendra (Barman *et al.*, 2022) [5].

2. Mechanisms and consequences of nonreproductive effect

The parasitism process includes several steps, including host search, selection, infection, and host adaptation to facilitate parasitoid production (Godfray, 1994 [13]. Vinson, 1998 [38]). System-wide, even if the parasitoid lineage is not well developed, various strategies can have different effects affecting the health of both the host and the parasitoid. To identify these mechanisms and their associated consequences, they proposed a unified and explanatory framework for future parasitoid conflict. It can be classified according to the modalities of parasitic sequence: (a) the host's seeking and accepting behavior before detecting the ovipositor, (b) injection (eg venom) or biological material by ovipositor, causes body injury (eg, symbiont, viral) factors; and (c) incomplete development of immature organisms (such as egg, larva, or pupa) after oviposition. Each of these methods affects its owner differently. These effects are listed in order of benefit to the host, including behavioral changes, developmental changes, reproductive changes, and death. Based on the process developed by each mechanism.

3. Non-Consumptive Effects

Non-consumptive interactions, also known as trait-mediated interactions, refer to the effects of natural enemies that do not involve prey or host consumption but cause costly defensive behavior in insects. These interactions are recognized as important components of ecological processes. In the context of parasitoids, non-drug interactions refer to sterile effects in which the host exhibits costly defensive strategies when a parasitoid is detected. These effects may occur before the

parasitoid inserts the ovipositor into the host or due to a failed attack in which the host survives. A well-known example is the eruption of aphids when attacked by a parasitoid in response to alarm pheromones released by the same insect. Many aphids disperse from plant to soil, and those that do not return to the plant may die of starvation, desiccation, or prey by ground arthropods (Gowling & van Emden, 1994 and Roitberg & Myers, 1979) [14, 29]. Direct contact between aphids and parasitoids can have similar effects, for example, on antennae (Ingerslew and Finke, 2017) [18]. Tamaki *et al.* (1970) [34] measured the incidence of population-level ineffectiveness in aphid populations using the pea aphid, *Acyrtosiphon pisum* and the parasitoid *Aphidius smithi*. They found that the female *A. smithi* construct (with its ovipositors removed to prevent parasitism) resulted in approximately 30 percent less aphid population growth compared to the conventional control without intervention. The presence of parasitoids can alter the development of the host, as indicated by an increase in the number of wings and offspring in the presence of female parasitoids (Sloggett & Weisser, 2002) [32]. Other non-destroying effects observed in the seed beetle *Mimosestes amicus* include the female covering the surviving eggs with additional eggs that fail to protect them from parasitism by *Uscana semifumipennis*. This defense strategy increases the cost of the host because production is lower in the insect infested insect compared to the control beetle (Deas & Hunter, 2012 [12]).

4. Mutilation and pseudoparasitism

When female parasitoids encounter a host, they may release ovipositors to assess the host's suitability or to eliminate competing offspring before laying (ovicide or larvicide). During this process, which may involve the injection of bacteria, venom, teratogenic cells, or other biological/chemical agents, the disease may eventually accept the host or be destroyed by predators, host defense behavior, competitors, or abiotic factors before laying eggs. For example, the parasitoid of the *Epinotia tedella* moth repels about 75% of the larvae (Munster-Swendsen, 2002) [26]. The eggs of parasitoids of the genus *Aphytis* and *Metaphycus* are usually destroyed by ants (Barzman & Daane, 2001 and Martinez-Ferrer *et al.* 2001, 2003) [6, 22]. An ovipositor insertion without ovulation causes two conflicts: mutilation and pseudo parasitism. Injury occurs due to damage to the host during ovipositor insertion, while pseudoparasitism involves injection of a substance that modifies the body but does not induce ovulation (Jones *et al.*, 1981; Munster-Swendsen, 1994) [20, 25].

Table 1: Major biological functions of venom from parasitoid wasps

Biological Functions	Wasp	Parasitism	Host
Paralysis			
pimplin	<i>Pimpla hypochondriaca</i>	Endo	<i>Lacanobia oleracea</i>
philanthotoxins	<i>Philanthus triangulum</i>	Ecto	<i>Schistocerca gregaria</i>
Brh-I & -II	<i>Bracon hebetor</i>	Ecto	<i>Diaprepes abbreviatus</i>
GABA, β -alanine, taurine	<i>Ampulex compressa</i>	Ecto	<i>Periplaneta americana</i>
Hemocyte inactivation			
VPr1	<i>Pimpla hypochondriaca</i>	Endo	<i>L. oleracea</i>
VPr3	<i>Pimpla hypochondriaca</i>	Endo	<i>L. oleracea</i>
Vn.11	<i>Pteromalus puparum</i>	Endo	<i>Pieris rapae</i>
VP P4, RhoGAP	<i>Leptopilina boulardi</i>	Endo	<i>Drosophila melanogaster</i>
calreticulin	<i>Cotesia rubecula</i>	Endo	<i>P. rapae</i>
	<i>Pteromalus puparum</i>	Endo	<i>P. rapae</i>
SERCA *	<i>Ganaspis</i> sp.1	Endo	<i>D. melanogaster</i>
Inhibition of Melanization			

LbSPNy	<i>Leptopilina bouvardi</i>	Endo	<i>D. melanogaster</i>
Vn50	<i>Cotesia rubecula</i>	Endo	<i>P. rapae</i>
Interrupting development			
Reprolysin	<i>Eulophus pennicornis</i>	Ecto	<i>L. oleracea</i>
Enhancing PDVs			
Vn1.5	<i>Cotesia rubecula</i>	Endo	<i>P. rapae</i>
Castration			
γ -glutamyl transpeptidase	<i>Aphidius ervi</i>	Endo	<i>Acyrtosiphon pisum</i>
Anti-microbial			
PP13, PP102, PP113	<i>Pteromalus puparum</i>	Endo	<i>P. rapae</i>

* sarco/ endoplasmic reticulum calcium ATPase. [Source: Moreau *et al.*, (2015). *Toxins*] ^[25]

5. Immune defense costs and aborted parasitism

Costs of protecting parasitoids against disease and failure of parasitoids often lay eggs in hosts unsuitable for the development of their offspring, resulting in death from disease at different developmental stages. Two terms are used to describe the negative aspects of breeding failure of the offspring: the cost of protection against disease and the removal of parasitic diseases. These elements represent a negative host treated by the host's immune system, or immature viruses before the virus dies, respectively.

6. Occurrence, condition dependence, and costs

Non reproductive effect between host parasitoids is common and found in different hosts and parasitoids. These effects have been reported in both holometabola (eg Lepidoptera, Coleoptera, Diptera) and hemimetabola (eg. Hemiptera) host taxa infect eggs, nymphs, larvae, pupae and adults. Some of the key observations are, - the prevalence and consequences of sexual dysfunction are associated with factors similar to those associated with death from disease. The characteristics of the host, the characteristics of the disease, ecological characteristics, environmental and other factors are effective in the formation and size of the gender deficiency. However, these conditions can affect growth and the absence of sex differences. For example, the mutilation and pseudoparasitism, mortality rate of *Bactrocera cucurbitae* pupae decreases with the age of the host. Additionally, some factors, such as the presence of an ant host, may reduce the negative effects of fixation-induced mutilation, but less so for reproductive influences. More research on the adverse effects of reproduction with infectious diseases, using the same principles and determining the probability of these effects, although there is less pattern and variation in developmental effects.

7. Ecological and evolutionary implications of nonreproductive effects

Parasitoids possess many behavioral and physiological characteristics that lead to varying purposes such as host finding, feeding and exploiting hosts. However, the phenomenon of non-reproduction cannot be considered a logical strategy that parasitoids develop to exploit or expand their hosts. However, from an evolutionary point of view, non-reproductive events can create favorable conditions for the formation of new host-parasitoid associations. This happens when parasitoids first encounter new species that have the potential and ability to adapt to find, develop, and reproduce on a new host (Poulin, 2011) ^[27]. These conditions are more likely to occur when pathogens with host-like ecological and physiological characteristics are abundant in the environment. Initially, poor decision making by parasitoids can be exacerbated and lead to adverse effects that transform parasitoids into evolutionary tools (Heimpel &

Mills, 2017) ^[17]. For example, Abram *et al.* (2014) ^[1]. Grow in this organization, avoid host by female. They transfer multiple copies of its genes to the next generation, reducing the frequency of adverse effects on the host. However, behavior patterns can be changed in order to minimize the negative effects in the short term, and physical behaviors that will increase addiction can be chosen to get rid of the offspring after this mistake. Non-reproductive effects that previously caused death in failed parasitoid development could pave the way for mutant parasitoid populations that can complete offspring in the disease type. Therefore, the unchanging initial event will result in some offspring, gradually reducing the selection pressure in the host to avoid oviposition. Theoretically, this process could lead to specialization in the parasitoid, thereby gaining the ability to attack new hosts (Stireman *et al.*, 2017, 2006) ^[33]. The role of sterile conditions in the formation of host diversity of the parasitoid depends on the ecological and physiological preadaptation developed by the host, the rate of encounter with new hosts, the genetics of adaptation in relationships, and subsequent health outcomes. There is currently anecdotal evidence of potential effects of non-productive parasitoids on host-parasitoid interactions between populations and communities (Mu'nster-Swendsen & Berryman, 2005) ^[24]. However, to better understand the importance of non-reproductive factors on parasitic death in direct and indirect interactions at the ecosystem level, theoretical approaches are developed mainly through modelling. Abram *et al.* (2016) ^[2] developed a model to investigate the effect of egg-restricted parasitoids or failure of host egg-induced parasitism. They found that abortion had a negative impact on the population growth of the host and, to a lesser extent, on the population growth of the parasitoids, especially when the female parasitoids had few eggs. Cassel *et al.* (2018) ^[21] investigated the population-level consequences of poor reproduction of parasitoids in the context of new associations of invasive hosts from local groups. They developed models to study parasitoid-mediated indirect transmission, identifying non-breeding between suitable hosts (coevolutionary associations) and unsuitable hosts (new associations) egg lays or the time limit without infection. Emerging models suggest that host deaths due to non-reproductive pathogens are directly related in a variety of ways, including overt competition, overt parasitism, overgrowth, and overt commensalism, depending on the abortive process of the virus and the extent of the virus' egg closure.

Parasitoids are common in terrestrial ecosystems and their parasitoids can have a significant impact on food webs (Hawkins & Sheehan, 1994) ^[16]. However, to date, there is no evidence of conflict's contributes to the structure and stability of ecological communities. Understanding the functional roles of this often-neglected species presents new challenges for public ecologists. Extending the current host-parasitoid wasp

population and community models to include infertility can provide a better understanding of the overall interactions that shape community structure, energy and performance. Additionally, it can reveal the cascade of non-reproductive effect.

8. Impacts of biological control agents on insect pests

Effects on the host by biological control agents is solely due to the death of the host due to feeding or insufficient emergence of parasitoid offspring (Abram *et al.*, 2016; Van Drescher, 1983) [2, 37]. These effects are often part of the effects of parasitoids on participants. Therefore, biocontrol researchers must measure and account for these effects on hosts.

8.1 Augmentative biocontrol: Innundative/augmentative release of parasitoids can be successful for short-term pest control, but most host dies due to lack of non-reproductive effect. The effect on reproduction in mass support used in submerged and augmented biocontrol programs may be uncertain. On the other hand, depletion of the host's immune system by the hyperparasitic may allow the use of other non-reproductive sources (Tena *et al.*, 2008) [35]. Moreover, the effects of not having offspring will lead to poor equipment or poor owners. For example, a dead host or an unhealthy host can produce weak parasitoids.

8.2. Conservation biocontrol: it is nothing but habitate manipulation for providing pollen, nectar, shelter to parasitoid. However, plant protection strategies that involve providing alternative hosts for parasitoids (Bernal, 2011) [7] can also be considered to protect parasitoids against non-target hosts.

8.3. Classical Biological Control: It is a kind of introduction of natural enemy from its original place of generation to a new place for biological pest control. Population (Heimpel & Mills, 2017) [17]. However, this hypothesis may not be valid if the severity of reproductive disadvantage is significant and target species that may support parasitoid species are often associated with the species. In the absence of a link between parasitoids, there may be significant and lasting effects on non-target species, we recommend including these effects as an additional measure in the evaluation of hosts of non-target species.

9. Future issues

The host-parasitoid population dynamics and trophic networks model should include these NRE. This will involve investigating whether this benefit can be used as a competitive strategy to increase the capacity of the parasitoid. Further research should be conducted to examine the effects of interactions such as communal hosts, interactions with predators and competitors on the frequency and magnitude of gender deficiency. There is a need for continuous development and use of quantitative and molecular methods to evaluate the occurrence of infertility in the field and to understand its effects on the population. It is important to investigate the role of beneficial bacteria and pathogenic bacteria in the immature parasitoids of their hosts.

10. Conclusion

Conflicts between parasitoids are often considered prohibitive, but they can provide health benefits.

Understanding the costs and benefits of these interactions is critical to the success of ecological and evolutionary perspectives and biological control programs. Model evaluation and reporting and further research will improve our understanding of the ecological impact and potential use of conflict in parasitoid interaction.

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