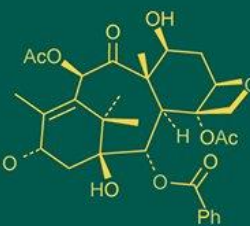
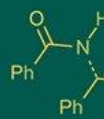
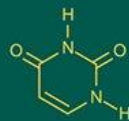


International Journal of Advanced Biochemistry Research



ISSN Print: 2617-4693
 ISSN Online: 2617-4707
 NAAS Rating (2026): 5.29
 IJABR 2026; SP-10(8): 189-195
www.biochemjournal.com
 Received: 05-06-2026
 Accepted: 06-07-2026

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Insect cannibalism: Mechanisms, evolutionary dynamics, and applications in agriculture

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DOI: <https://www.doi.org/10.33545/26174693.2026.v10.i8Sc.9424>

Abstract

Cannibalism in insects extends far beyond an emergency response to starvation or overpopulation. Instead, it serves as a dynamic, highly regulated ecological strategy driven by complex physiological, biochemical, and molecular mechanisms. This review examines how key environmental factors, such as nutrient deficits, population density, developmental stages, and host plant quality, interact to trigger conspecific predation. Recent insights into the metabolic pathways, hormonal controls, gut microbiome shifts, and genetic networks that govern these aggressive interactions are synthesised. Notably, plant-mediated effects are highlighted, where induced crop defences force herbivorous insects toward cannibalism, indirectly reducing crop damage. Additionally, the evolutionary trade-offs of this behaviour, including pathogen transmission risks, kin selection, and defensive chemical adaptations, are analysed. Finally, practical applications for integrated pest management (IPM) and commercial insect rearing are explored, while critical knowledge gaps are identified to guide future research.

Keywords: Cannibalism, herbivorous insects, nutritional ecology, gut microbiota, plant-mediated defence, integrated pest management, *Spodoptera*, behavioural ecology

Introduction

Cannibalism, the act of killing and consuming an individual of the same species, is a common ecological phenomenon observed across the animal kingdom. Earlier, it was often regarded as an unusual behaviour or simply an artefact of laboratory conditions where insects were forced into close contact (Fox, 1975) [7]. However, decades of research have shown that cannibalism is a naturally occurring behaviour with important ecological and evolutionary functions. It has now been reported in more than 1,300 animal species, including a wide range of insects (Fox, 1975; Santana *et al.*, 2012) [7, 21].

Among herbivorous insects, cannibalism is more common than once believed. It has been reported in over 130 non-carnivorous insect species belonging to several major orders, including Coleoptera, Lepidoptera, Orthoptera, Hemiptera, Diptera, Hymenoptera, and Blattodea (Richardson *et al.*, 2010; Geniesse, 2022) [18, 8]. Most of these records involve phytophagous insects, particularly caterpillars and leaf or seed feeding beetles, which account for the majority of documented cases (Richardson *et al.*, 2010) [18].

Although these insects feed mainly on plants, plant tissues do not always provide a balanced supply of nutrients. They are often deficient in nitrogen, proteins, sodium, and certain lipids that are essential for normal growth and development. Under such conditions, feeding on a conspecific can provide nutrients that are otherwise difficult to obtain from the host plant, improving growth, development, and survival (Orrock *et al.*, 2017; Randall *et al.*, 2023; Santiago-Rosario *et al.*, 2023) [16, 17, 22]. This behaviour is particularly common when host plants are scarce, heavily damaged, or of poor nutritional quality, allowing larvae to survive and complete development under otherwise unfavourable conditions (Snyder *et al.*, 2000; Vergara *et al.*, 2016; He *et al.*, 2021; Hao *et al.*, 2023) [24, 26, 10, 9]. Beyond its benefits to individual survival, cannibalism can also reduce competition for limited resources and influence the size and age structure of insect populations (Fox, 1975; Fernandez *et al.*, 2020; Boots *et al.*, 2021) [7, 6, 2].

However, engaging in intraspecific predation involves significant physiological and evolutionary trade-offs. While cannibals gain immediate energetic rewards, eliminate potential competitors, and enhance overall survival fitness

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(Chapman *et al.*, 1999; Bharathi *et al.*, 2023) ^[3, 1], they also incur substantial costs. These include retaliatory injuries, exposure to horizontal and vertical pathogen transmission, and reduced inclusive fitness when preying on genetic kin (Sadeh & Rosenheim, 2016; Van Allen *et al.*, 2017; Long, 2022) ^[20, 25, 11].

Recent advances across biochemistry, molecular genetics, endocrinology, and multi-trophic ecology have uncovered intricate mechanisms regulating this behavior. These include specific genetic factors and nutrient-sensing signaling pathways linked to intraspecific predation (Ryuda *et al.*, 2008) ^[19], gut microbiome-endocrine interactions (such as gut-derived *Escherichia* sp. modulating Juvenile Hormone levels to suppress cannibalistic behavior) (Du *et al.*, 2023) ^[5], plant defense-induced cannibalism that effectively reduces herbivory (Orrock *et al.*, 2017, Long, 2022) ^[16], and non-toxic chemical cloaking defenses utilized by parents or eggs to evade predation (Narasimha *et al.*, 2019; Vijendravarma, 2023) ^[15, 27].

In this review, we summarize current knowledge of the ecological, physiological, biochemical, and molecular mechanisms that influence insect cannibalism. We examine the environmental factors that promote this behaviour, the roles of host plants and microbial symbionts, its implications for disease transmission and population dynamics, and the adaptations that insects have evolved to minimize its costs. Particular attention is given to economically important agricultural pests such as *Spodoptera frugiperda* (Mbuji *et al.*, 2022; Bharathi *et al.*, 2023) ^[13, 1] and *Helicoverpa armigera* (Sigsgaard *et al.*, 2002; Vergara *et al.*, 2016) ^[23, 26]. By bringing together findings from different areas of insect biology, this review highlights the ecological importance of cannibalism. It discusses how this behaviour may be used to support integrated pest management and insect mass-rearing programmes.

2. Proximate Ecological Triggers and Environmental Drivers

2.1 Food Deprivation and Starvation

Food shortage is one of the most common and important factors that trigger cannibalism in insects. When host plants become scarce or completely depleted, insects experience severe nutritional stress, which often leads to major changes in their behaviour and physiology (Fox, 1975; Santana *et al.*, 2012; Geniesse, 2022) ^[7, 21, 8].

In many lepidopteran pests, starvation rapidly promotes aggressive interactions among larvae. For example, 4th-6th-instar larvae of *Spodoptera frugiperda* readily attack and consume smaller conspecifics when food is no longer available (Mbuji *et al.*, 2022) ^[13]. Cannibalism provides an immediate nutritional benefit, with each consumed larva extending survival by approximately two days under starvation conditions (He *et al.*, 2021) ^[10]. Studies have also shown that starving larvae that consume only a few conspecifics can survive long enough to complete larval development, pupate successfully, and emerge as fertile adults capable of reproduction (Chapman *et al.*, 1999; Bharathi *et al.*, 2023) ^[3, 1].

A similar response has been observed in *Spodoptera litura*. Starved larvae become noticeably more aggressive and are much more likely to attack conspecifics. Interestingly, this behavioural change is accompanied by changes in gene expression in the larval brain, suggesting that hunger-induced cannibalism is regulated through specific molecular pathways

rather than being a simple behavioural response to food shortage (Ryuda *et al.*, 2008) ^[19].

2.2 Nutritional Imbalance

Cannibalism is not necessarily a response to complete food deprivation. In many insect species, it occurs even when food is available but does not adequately meet their nutritional requirements. Since plant tissues are often deficient in several essential nutrients, feeding on a conspecific provides an alternative source of these limiting nutrients. This nutritional supplement helps insects maintain normal growth, development, and physiological functions when their regular plant-based diet is inadequate (Snyder *et al.*, 2000; Randall *et al.*, 2023) ^[24, 17].

Macronutrient Balance (Protein: Carbohydrate Ratios):

The balance between dietary protein and carbohydrates plays an important role in determining cannibalistic behaviour. In *Trichoplusia ni*, larvae reared on protein-deficient, carbohydrate-rich diets began cannibalising one another within the first few days of feeding. In contrast, larvae fed protein-rich, but carbohydrate-poor diets showed a slower initial response, although the total number of cannibalistic events eventually became even higher after prolonged feeding. The lowest levels of cannibalism and the highest larval survival were observed when protein and carbohydrate were supplied in balanced proportions, indicating that nutritional balance can greatly reduce aggressive interactions among larvae (Randall *et al.*, 2023) ^[17].

Sodium (Na⁺) limitation: Sodium is essential for nerve function, muscle activity, and maintaining osmotic balance, but it is generally present in very low concentrations in plant tissues. As a result, many herbivorous insects experience chronic sodium deficiency. Experimental studies have shown that larvae of the bordered patch butterfly, *Chlosyne lacinia*, displayed significantly higher levels of sibling cannibalism when they fed on sodium-deficient *Helianthus annuus* plants (Santiago-Rosario *et al.*, 2023) ^[22]. Similar responses have also been reported in Mormon crickets (*Anabrus simplex*) and other herbivorous insects, including *Melanoplus differentialis* and *Helicoverpa armigera*, suggesting that cannibalism may serve as an effective strategy for obtaining limiting mineral nutrients (Richardson *et al.*, 2010; Santiago-Rosario *et al.*, 2023) ^[18, 22].

Protease inhibitors: Plant defensive compounds can also promote cannibalism indirectly. Many plants produce proteinase inhibitors through jasmonate-mediated defence pathways. These compounds interfere with digestive proteases in the insect gut, reducing protein digestion and creating a condition similar to protein starvation. Under such circumstances, larvae may switch to feeding on conspecifics because animal tissue provides a readily digestible and protein-rich food source (Orrock *et al.*, 2017, Long, 2022) ^[16, 11].

2.3 Population Density, Size Asymmetry, and Developmental Stage

Apart from food availability and nutrition, cannibalism is strongly influenced by population structure. Factors such as larval density, differences in body size, and developmental stage determine how frequently individuals encounter one

another and which individuals are most likely to become victims.

Population density: As population density increases, insects encounter conspecifics more frequently while competing for the same resources. This combination of increased contact and stronger competition often leads to higher rates of cannibalism (Fox, 1975; Fernandez *et al.*, 2020) ^[7,6]. In predatory insects such as the damselfly bug (*Nabis pseudosolus*) and the ladybird beetle (*Harmonia axyridis*), cannibalism becomes more common at higher larval densities even when sufficient prey is available. These findings suggest that cannibalism can function as a density-dependent mechanism that naturally regulates population size, rather than simply being a response to starvation (Michaud, 2003; Fernandez *et al.*, 2020; Boots *et al.*, 2021) ^[14,6,2].

Size-structured cannibalism: Differences in body size are among the strongest predictors of cannibalistic interactions. Larger and older larvae usually dominate smaller individuals and commonly prey upon younger instars, eggs, or immobile pupae (Fox, 1975; Richardson *et al.*, 2010; Sigsgaard *et al.*, 2002; Collie *et al.*, 2013; Hao *et al.*, 2023) ^[7,18,23,4,9]. In *Spodoptera frugiperda*, predation by late instars on younger larvae follows a Holling Type II functional response, with consumption increasing as prey density rises until it reaches a plateau because of handling time limitations (Mbuji *et al.*, 2022) ^[13].

Exceptions to size dominance: Although larger individuals generally have an advantage, body size alone does not always determine the outcome of cannibalistic interactions. In *Helicoverpa armigera*, early-instar larvae have occasionally been observed feeding on haemolymph leaking from injured or dying late-instar larvae. These observations indicate that injury and weakened physical condition can sometimes outweigh the advantage of larger body size, allowing smaller larvae to exploit otherwise inaccessible food resources (Richardson *et al.*, 2010; Vergara *et al.*, 2016) ^[18,26].

3. Biochemical, Metabolic, and Endocrine Mechanisms

3.1 Metabolic Reprogramming During Cannibalism

Cannibalism provides more than just an immediate source of energy during starvation. Feeding on conspecifics causes a series of metabolic adjustments that help insects utilize animal-derived nutrients more efficiently. Studies using transcriptomics, quantitative PCR, and metabolomic analyses in *Spodoptera frugiperda*, *Spodoptera litura*, and *Helicoverpa armigera* have shown that cannibalism is accompanied by coordinated changes in several key metabolic pathways (Snyder *et al.*, 2000; Vergara *et al.*, 2016) ^[24,26].

Amino acid sensing and TORC1 activation

One of the earliest responses to conspecific feeding is the activation of amino acid sensing pathways. Under starvation, cannibalistic larvae show increased expression of the lysosomal amino acid sensor SLC38A9, which activates the mechanistic target of rapamycin complex 1 (TORC1) signalling pathway. At the same time, amino acid transporters such as SLC3A2 and SLC36A1 are also upregulated, allowing amino acids released from consumed conspecifics to be transported rapidly into cells. Together, these responses restore protein synthesis while reducing excessive autophagy,

helping larvae recover from severe nutritional stress (Vergara *et al.*, 2016; Ryuda *et al.*, 2008) ^[26,19].

Activation of gluconeogenesis

Cannibalism also changes the way energy is produced during starvation. Following conspecific feeding, the expression of phosphoenolpyruvate carboxykinase (PEPCK), the rate-limiting enzyme in gluconeogenesis, increases markedly. Enzymes such as aspartate aminotransferase and pyruvate carboxylase provide the necessary substrates by converting amino acids obtained from consumed larvae into intermediates that are ultimately used for glucose production. This metabolic adjustment helps maintain energy balance when carbohydrates are limited (Vergara *et al.*, 2016; Randall *et al.*, 2023) ^[26,17].

Suppression of glycolysis

While gluconeogenesis is enhanced, glycolysis is simultaneously reduced. The expression of important glycolytic enzymes, including pyruvate kinase (PK) and ATP-dependent phosphofructokinase (PFK), declines following cannibalism. This shift reduces glucose breakdown and instead favours the recycling of amino acids and the synthesis of glucose from non-carbohydrate sources, allowing insects to survive for longer periods under food-limited conditions (Vergara *et al.*, 2016) ^[26].

Limitations of an exclusive cannibalistic diet

Although cannibalism is beneficial during periods of starvation, it cannot support normal development over the long term. Two-dimensional nuclear magnetic resonance (2D-NMR) metabolomic analysis of *Helicoverpa armigera* showed that larvae fed only on conspecifics had significantly lower levels of soluble carbohydrates, glycerol phosphate, and several essential amino acids, including lysine, glycine, leucine, isoleucine, valine, proline, glutamine, and threonine, compared with larvae reared on their natural plant diet (Vergara *et al.*, 2016) ^[26]. These findings indicate that cannibalism is primarily a short-term survival strategy rather than a nutritionally complete feeding habit (Snyder *et al.*, 2000; Vergara *et al.*, 2016) ^[24,26].

3.2 Microbiome-Endocrine Interactions

Recent studies have shown that gut microorganisms play an important role in regulating cannibalistic behaviour through their effects on the insect endocrine system. In *Spodoptera exigua*, disruption of the normal gut microbiota results in a substantial decline in juvenile hormone (JH) levels, which is accompanied by a marked increase in larval cannibalism. Researchers identified a beneficial gut bacterium, *Escherichia* sp. strain SePC-12, from populations showing low levels of cannibalism. When this bacterium was reintroduced into aggressive larvae, juvenile hormone levels returned to normal and cannibalistic behaviour was greatly reduced. Similar responses were observed in *Spodoptera frugiperda* and *Helicoverpa armigera*. In addition, experiments using gnotobiotic larvae confirmed that SePC-12 directly contributes to maintaining juvenile hormone homeostasis, thereby reducing aggressive interactions among conspecifics (Du *et al.*, 2023) ^[5]. These findings highlight the important role of the gut microbiome in linking nutrition, hormonal regulation, and cannibalistic behaviour.

3.3 Genetic Basis of Hunger-Induced Cannibalism

Cannibalistic behaviour is influenced not only by environmental conditions but also by genetic factors. In *Spodoptera litura*, differential display RT-PCR identified a novel 779-bp gene that was specifically upregulated in the brains of highly cannibalistic larvae after 48 hours of starvation (Ryuda *et al.*, 2008) [19]. Under normal feeding conditions, the expression of this gene remained low, but during food deprivation its transcript level increased by approximately 2.6-fold. Further evidence for a genetic component comes from selection experiments in which 17 successive generations were bred for reduced cannibalism. This selection reduced the frequency of cannibalistic behaviour from 24.5% to only 3.2%, indicating that hunger-induced aggression has a substantial heritable component (Ryuda *et al.*, 2008; Boots *et al.*, 2021) [19, 2]. Taken together, these studies suggest that insect cannibalism is shaped by both environmental cues and inherited behavioural traits, allowing populations to respond and adapt to changing environmental conditions.

4. Plant-Mediated Cannibalism and Multi-Trophic Interactions

Plants are active participants in modulating herbivore-cannibal interactions. Induced plant defenses alter herbivore behavior, effectively turning pest insects against one another (Orrock *et al.*, 2017; Long 2022; Geniesse, 2022) [16, 11, 8].

4.1 Jasmonate-Induced Plant Defenses and Herbivore Behavior

Treating tomato plants (*Solanum lycopersicum*) with methyl jasmonate (MeJA) induces systemic resistance, elevating anti-herbivore defense proteins (e.g., proteinase inhibitors) and toxic secondary metabolites (Orrock *et al.*, 2017) [16]. When exposed to MeJA-induced foliage, *Spodoptera exigua* and *Helicoverpa zea* caterpillars initiate cannibalism significantly earlier and consume higher proportions of conspecifics compared to those feeding on non-induced control plants (Orrock *et al.*, 2017; Long, 2022) [16, 11].

4.2 Benefits of Defence-Induced Cannibalism to Host Plants

Plant-induced cannibalism provides several indirect advantages to host plants in addition to their conventional defence mechanisms (Orrock *et al.*, 2017; Long, 2022) [16, 11].

Reduction in herbivore populations: Cannibalism lowers the number of feeding larvae within a plant population. As individuals consume one another, the local herbivore population declines, resulting in less overall feeding pressure and reduced leaf damage (Mbuji *et al.*, 2022; Orrock *et al.*, 2017) [13, 16].

Reduced feeding by surviving larvae: Larvae that have consumed conspecifics often feed less on plant tissues afterwards. Because animal tissue is rich in nutrients, these larvae satisfy part of their nutritional requirements through cannibalism and show a lower demand for foliage. As a consequence, plants in which defence responses promote cannibalism retain considerably more leaf tissue than untreated plants. In some studies, plants experiencing high levels of defence-induced cannibalism retained more than five times the leaf biomass of heavily damaged control plants (Orrock *et al.*, 2017; Long, 2022) [16, 11].

4.3 Comparative Efficacy and Meta-Analytic Evidence

Evidence from several experimental systems highlights the ecological importance of plant-mediated cannibalism. In *Helicoverpa zea*, the reduction in leaf damage resulting from defence-induced cannibalism was comparable to that achieved by infection with *Helicoverpa zea* single nucleopolyhedrovirus (HzSNPV), demonstrating that changes in herbivore behaviour can protect plants as effectively as some natural biological control agents (Orrock *et al.*, 2022; Long, 2022) [16, 11].

Support for this concept also comes from broader comparative studies. A meta-analysis covering multiple groups of phytophagous insects found that host plant quality is one of the most consistent factors influencing cannibalistic behaviour. Insects feeding on nutritionally poor hosts, plants with higher concentrations of defensive compounds, or under conditions of limited host availability were consistently more likely to cannibalize conspecifics (Geniesse, 2022) [8]. Together, these findings indicate that plant-induced nutritional and physiological stress plays a major role in promoting cannibalism, ultimately contributing to the natural suppression of herbivore populations.

5. Disease Dynamics and Epidemiological Implications

The interaction between cannibalism and infectious pathogens represents a major eco-evolutionary trade-off (Sadeh & Rosenheim, 2016; Van Allen *et al.*, 2017) [20, 25]. While conspecific consumption provides immediate energetic gains, it also acts as a powerful vector for pathogen dispersal or, conversely, a mechanism for disease suppression within pest populations (Sadeh & Rosenheim, 2016; Long, 2022) [20, 11].

5.1 Horizontal transmission through cannibalism

Cannibalism is an effective route for the horizontal transmission of several insect pathogens. In species such as *Spodoptera frugiperda*, *Spodoptera exigua*, and *Helicoverpa armigera*, healthy larvae that consume virus-infected conspecifics readily acquire nucleopolyhedroviruses (NPVs) or granuloviruses, often resulting in high mortality (Van Allen *et al.*, 2017; Long, 2022) [25, 11]. Viral infection causes noticeable changes in the behaviour and physiology of infected larvae, including reduced activity, impaired movement, poor coordination, and the characteristic climbing behaviour known as tree-top disease. These behavioural changes make infected larvae easier targets for healthy conspecifics, thereby increasing the likelihood of pathogen transmission through cannibalism (Chapman *et al.*, 1999; Richardson *et al.*, 2010; Long, 2022) [3, 18, 11].

5.2 Dose-Dependent Effects on Cannibals

The risk of infection following cannibalism depends largely on the amount of infected tissue consumed. In *Spodoptera frugiperda*, larval mortality increases with the number of conspecifics infected with *Spodoptera frugiperda* multiple nucleopolyhedrovirus (SfMNPV) that are consumed (Chapman *et al.*, 1999; Long, 2022) [3, 11]. Consuming several infected larvae introduces a much higher viral load, which can overcome the protective barriers of the larval midgut and allow rapid viral replication. As the infection progresses, it eventually results in lethal polyhedrosis (Chapman *et al.*, 1999; Van Allen *et al.*, 2017) [3, 25].

5.3 Influence on Vertically Transmitted Pathogens

Cannibalism may also affect the persistence of pathogens that are transmitted from parent to offspring. Both theoretical studies and experimental evidence suggest that high levels of cannibalism can increase the long-term prevalence of vertically transmitted pathogens within insect populations. One possible explanation is that cannibalism alters population turnover by removing uninfected or weaker individuals, while infected adults continue transmitting pathogens to their offspring. Over time, this process can maintain high levels of infection within the population and contribute to a stable host-pathogen relationship across generations (Sadeh & Rosenheim, 2016) [20].

5.4 Disease Suppression Through Population Thinning

Although cannibalism can facilitate pathogen transmission, it can also reduce disease under certain ecological conditions. In populations where disease outbreaks depend on high host density, cannibalism lowers the number of susceptible individuals and may reduce the population below the threshold required for an epidemic to develop (Van Allen *et al.*, 2017) [25]. In addition, when cannibals consume infected larvae before they rupture and release infectious occlusion bodies into the environment, they effectively remove an important source of infection and limit further pathogen spread (Van Allen *et al.*, 2017; Long, 2022) [25, 11]. Therefore, the overall impact of cannibalism on disease dynamics depends on the balance between pathogen transmission through infected prey and the reduction of environmental pathogen reservoirs.

6. Evolutionary Trade-Offs, Kin Selection, and Anti-Cannibalism Defences

6.1 Spatial Structure, Kin Selection, and Life-Stage Defences

Although cannibalism can provide an immediate nutritional advantage, it is associated with important evolutionary costs. According to Hamilton's rule ($rB > C$), consuming closely related individuals reduces inclusive fitness because it decreases the transmission of shared genes to future generations (Boots *et al.*, 2021) [2]. As a result, natural selection has favoured mechanisms that reduce cannibalism among relatives while still allowing the behaviour to occur when food is scarce and survival is at risk.

The spatial arrangement of individuals within a population is one of the factors that influences cannibalistic behaviour. Experimental evolution studies in the Indian meal moth, *Plodia interpunctella*, demonstrated that restricting larval movement and increasing spatial viscosity resulted in a gradual decline in cannibalism over successive generations. Under these conditions, neighbouring larvae are more likely to be siblings or close relatives, making cannibalism costlier in terms of inclusive fitness (Boots *et al.*, 2021) [2].

Many insects also possess mechanisms for recognizing kin before attacking. Species such as *Harmonia axyridis* and *Tribolium confusum* use chemical cues to distinguish relatives from unrelated individuals and are less likely to cannibalize close kin (Michaud, 2003; Snyder *et al.*, 2000) [14,24]. In contrast, species such as *Cycloneda sanguinea* and *Olla v-nigrum* show little evidence of kin discrimination. Since these insects naturally lay their eggs in dispersed locations, siblings are less likely to develop together, reducing the evolutionary advantage of maintaining an active

kin-recognition system (Michaud, 2003; Martini *et al.*, 2015) [14,12].

6.2 Stage-Specific Anti-Cannibalism Defences

The risk of cannibalism is not the same throughout an insect's life cycle. Consequently, different developmental stages have evolved their own structural, chemical, and behavioural adaptations that reduce the likelihood of being attacked by conspecifics (Vijendravarma, 2023) [27].

Egg stage: Eggs depend mainly on passive defence mechanisms. These include wax coatings rich in cuticular hydrocarbons that conceal the eggs, the production of infertile trophic eggs that divert newly hatched larvae, elevated egg stalks, protective egg cases, egg clustering, maternal guarding, and synchronized hatching, all of which reduce the chances of egg cannibalism (Sigsgaard *et al.*, 2002; Collie *et al.*, 2013; Narasimha *et al.*, 2019; Hao *et al.*, 2023; Vijendravarma, 2023) [23,4, 15, 9].

Larval stage: Larvae reduce the risk of cannibalism through both developmental and behavioural strategies. Rapid growth and synchronised development help minimise size differences within a cohort, thereby reducing opportunities for larger larvae to prey on smaller ones (Richardson *et al.*, 2010; Fernandez *et al.*, 2020) [18, 6]. Some wood-boring larvae, such as *Monochamus sutor*, produce acoustic mandibular scraping sounds that discourage conspecifics from entering occupied galleries. Likewise, ladybird larvae leave hydrocarbon trail markers that discourage females from laying eggs in the same location, thereby reducing the likelihood of future cannibalistic encounters (Vijendravarma, 2023) [27].

Pupal stage: During moulting and pupation, insects are largely immobile and therefore highly vulnerable to attack. To reduce this risk, many species pupate in protected locations such as underground chambers, silk cocoons, or heavily sclerotised pupal cells, where they remain isolated from feeding larvae (Richardson *et al.*, 2010) [18].

Adult stage (sexual cannibalism): In species where sexual cannibalism occurs, males have evolved several behavioural adaptations to improve their chances of surviving mating. These include offering nuptial gifts, traumatic insemination, rapid escape immediately after copulation, and tonic immobility (thanatosis), all of which reduce the risk of being consumed by females before or after mating (Vijendravarma, 2023) [27].

6.3 Non-Visual Chemical Deception: Egg Cloaking in *Drosophila melanogaster*

One of the most remarkable anti-cannibalism strategies reported in insects is the chemical camouflage used by *Drosophila melanogaster*. Instead of relying on toxic compounds to deter predators, females protect their eggs by covering them with non-toxic chemical cues that prevent recognition by conspecific larvae (Narasimha *et al.*, 2019) [15].

The eggshell of *D. melanogaster* consists of four layers: the outer exochorion, the endochorion, a very thin internal wax layer measuring approximately 4-5 nm, and the inner vitelline membrane. High-resolution APPI-FT-ICR mass spectrometry has shown that this wax layer contains thirteen

parental cuticular hydrocarbons, including 7-tricosene (7-T), 11-cis-vaccenyl acetate (cVA), 7,11-nonacosadiene (7,11-ND), and 7,11-heptacosadiene (7,11-HD) (Narasimha *et al.*, 2019) [15].

Among these hydrocarbons, 7,11-HD plays a particularly important role in preventing egg cannibalism. Larvae generally ignore intact eggs coated with this compound. However, when the wax layer is removed using hexane or when the larval chemosensory gene *pickpocket 23* (*ppk23*) is mutated, egg consumption increases dramatically (Narasimha *et al.*, 2019; Vijendravarma, 2023) [15, 27].

Further studies have shown that 7,11-HD functions both as a physical barrier and as a chemical camouflage. The wax layer seals the vitelline membrane, preventing nutrients from leaking out, while at the same time masking the gustatory signals that would normally stimulate larval feeding. This protective effect was further demonstrated by coating yeast droplets with synthetic 7,11-HD, which significantly reduced larval feeding. These findings indicate that 7,11-HD effectively conceals eggs from foraging larvae by acting as both a physical shield and a chemical cloak (Narasimha *et al.*, 2019; Vijendravarma, 2023) [15, 27].

7. Applied Perspectives in Agriculture and Insect Rearing

A better understanding of the physiological and ecological factors that drive cannibalism has created new opportunities for its practical use in agriculture and insect production systems. Rather than viewing cannibalism only as a cause of mortality, researchers are increasingly exploring ways to manage or exploit this behaviour to improve integrated pest management (IPM) and the efficiency of mass insect rearing (Richardson *et al.*, 2010; Geniesse, 2022; Bharathi *et al.*, 2023) [18, 8, 1].

7.1 Optimizing Mass Rearing Systems

Cannibalism is one of the major challenges in the large-scale rearing of insects. It contributes substantially to larval mortality in commercial production systems used for beneficial insects such as ladybird beetles and lacewings, as well as in colonies of agricultural pests that are maintained for research purposes, including the fall armyworm. High levels of conspecific predation reduce survival, lower production efficiency, and increase the overall cost of rearing (Richardson *et al.*, 2010; Geniesse, 2022) [18, 8].

One practical approach to reducing cannibalism is improving the nutritional quality of larval diets. Studies have shown that supplementing early-instar diets with small amounts of conspecific eggs, trophic eggs, or key nutrients such as β -carotene and high-quality proteins can improve larval development, restore normal adult body size, and increase adult emergence from approximately 48% to more than 90% in *Harmonia axyridis* (Snyder *et al.*, 2000; Hao *et al.*, 2023) [24, 9]. These findings demonstrate that providing a nutritionally balanced diet can substantially reduce the tendency of larvae to cannibalize one another.

Another promising strategy involves manipulation of the gut microbiome. Beneficial microorganisms such as *Escherichia* sp. SePC-12 help maintain normal juvenile hormone levels during larval development, which in turn reduces aggressive and cannibalistic behaviour (Du *et al.*, 2023) [5]. Incorporating such beneficial symbionts into artificial diets or rearing protocols may reduce the need for labour-intensive methods such as individual isolation, making mass-rearing systems more efficient and cost-effective.

7.2 Crop Resistance and Pest Suppression

Plant-mediated cannibalism also has potential applications in crop protection. Inducing natural plant defence responses through compounds such as methyl jasmonate (MeJA) can indirectly influence the behaviour of herbivorous insects. Studies have shown that major lepidopteran pests, including *Spodoptera frugiperda*, *Spodoptera exigua*, and *Helicoverpa zea*, are more likely to cannibalise conspecifics when feeding on plants with activated jasmonate defence pathways (Orrock *et al.*, 2017; Long, 2022) [16, 11].

This change in behaviour offers two important advantages for pest management. First, cannibalism reduces pest populations through self-thinning, thereby lowering the number of larvae feeding on the crop. Second, surviving larvae generally consume less foliage because they obtain part of their nutritional requirements from conspecifics. Together, these effects reduce crop damage and may improve the effectiveness of biological control programmes while decreasing dependence on synthetic insecticides (Orrock *et al.*, 2017; Long, 2022) [16, 11].

8. Conclusion and Future Directions

Cannibalism is a common and highly flexible behaviour that plays an important role in the ecology and evolution of insects. Research over the past several decades has shown that this behaviour is influenced by a wide range of interacting factors, including nutritional status, host plant chemistry, metabolic and endocrine regulation, gut microbial communities, population structure, and environmental conditions (Vergara *et al.*, 2016; Orrock *et al.*, 2017; Du *et al.*, 2023; Randall *et al.*, 2023) [26, 16, 5, 17]. Rather than being simply a response to starvation, cannibalism is now recognized as an adaptive strategy that helps insects cope with changing environments. In doing so, it influences individual survival, population dynamics, physiological processes, and the transmission of insect pathogens.

At the physiological level, cannibalism is accompanied by substantial metabolic adjustments. During food deprivation, insects increase the expression of amino acid transporters such as SLC38A9 and activate gluconeogenic enzymes including phosphoenolpyruvate carboxykinase (PEPCK), allowing nutrients obtained from conspecifics to be efficiently utilized. At the same time, beneficial gut microorganisms such as *Escherichia* sp. SePC-12 influence juvenile hormone regulation, helping to moderate aggressive and cannibalistic behaviour (Ryuda *et al.*, 2008; Vergara *et al.*, 2016; Du *et al.*, 2023) [19, 26, 5]. Studies on plant-mediated defences and egg-cloaking mechanisms, such as the protective role of 7,11-heptacosadiene (7,11-HD) in *Drosophila melanogaster*, further demonstrate how evolutionary pressures have shaped both the occurrence of cannibalism and the development of strategies that reduce its risks (Orrock *et al.*, 2017; Narasimha *et al.*, 2019; Vijendravarma, 2023) [16, 15, 27].

Although considerable progress has been made, several important questions remain unanswered. Addressing these gaps will improve our understanding of insect behavioural ecology and may also contribute to the development of more effective and sustainable pest management strategies.

Future Research Priorities

Neural regulation of cannibalism: Future studies should identify the neural circuits operating downstream of the

ppk23 gustatory receptor to better understand how contact chemosensory signals are processed during egg recognition and how these pathways promote or suppress cannibalistic behaviour

Microbiome-endocrine interactions: Further research is needed to identify the metabolites produced by beneficial gut bacteria and determine how these compounds interact with the corpora allata to regulate juvenile hormone synthesis and influence aggressive behaviour.

Field-scale evaluation in IPM: Large-scale field studies are required to evaluate whether synthetic plant defence elicitors can consistently induce cannibalism under natural conditions and whether this approach can suppress pest populations without negatively affecting crop productivity across different agroecosystems.

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