Immune and defense mechanisms in representatives of Blattodea and Orthoptera: a review

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Abstract: Among insects orders, Blattodea and Orthoptera are characteristic with their high significance to human habitation, as posing medical and agricultural problems. Representatives of Blattodea have an important role as carriers of a number of infectious diseases in humans and animals, and are directly related to human life and activities. On the other hand Orthoptera are very significant as agricultural pests that cause great damage to plants. The study of the mechanisms of immune defense and the processes related to the response against pathogenic infections in these two orders is of interest in order to more fully clarify the possibilities for management and control of their populations. This review summarizes the information on the defense mechanisms (hemocytes, antimicrobial peptides, pathogen recognition, signaling pathways, immune and antiviral responses) studied in representatives of these two orders. The list includes 30 species of cockroaches and termites and 59 orthopteran species, and focuses on species with medical significance (Periplaneta americana, Blattella germanica) and insect pests for agriculture such as Locusta migratoria and Schistocerca gregaria.

Keywords: orthopterans, cockroaches, termites, insect immunity

Introduction

Among the representatives of Blattodea, cockroaches are the most common pests in human dwellings. They are found in sewers, where they feed on waste and human feces and can spread a number of parasites and pathogens in the environment (Cotton et al. 2000, Pai et al. 2005). In addition, they contaminate food by leaving feces and bacteria that can cause food poisoning (Che Ghani et al. 1993), but can also carry bacteria, fungi and other pathogens in infected areas (Czajka et al. 2003, Kopanic 1994). Their nocturnal lifestyles and habitats make them ideal carriers of various infections (Allen 1987). For example, a study of Periplaneta americana (Linnaeus, 1758) shows that its individuals in a very high percentage carry a number of bacteria - Escherichia coli (86.7%), Proteus vulgaris (73.3%), Bacillus cereus (66.7%), Streptococcus faecalis (60%), Staphylococcus aureus (60%), Enterobacter cloacae (53.3%), Shigella spp. (33.3%), Serratia spp. (13.3%) and Staphylococcus epidermidis (6.7%) (Feizhaddad et al. 2012). In the cockroaches P. americana and Blattella germanica (Linnaeus, 1767), 25 species of bacteria have been isolated from hospital premises, of which 22 were gram-negative, and it was found that the cockroaches were more prone to carry pathogenic bacteria internally (84.3%) than on their body surface (64.1%) (Fakoorziba et al. 2010).
A number of parasites have been found on the surface or inside cockroaches, and some studies have shown that exposure to cockroach antigens may play an important role in asthma-related health problems (Montresor et al. 1998, Mott 1989). These insects, inhabiting various places and objects in people's houses (toilets, salons, kitchens and bedrooms) are potential reservoirs of a number of parasites of medical significance, transmitted through the surface of their bodies. These include mainly: cysts of amoebae (*Entamoeba hystolitica*), oocysts of coccidians (*Cryptosporidium parvum*, *Cyclospora cayetenensis*, *Isospora belli*), cysts of the protozoan *Balantidium coli*, eggs, larvae and adults of parasitic worms from the nematode group (*Ascaris lumbricoides*, *Anchylostoma duodenale*, *Enterobius vermicularis*, *Trichuris trichura*, *Strongyloides stercoralis*) (El-Sherbini & El-Sherbini 2011).

The order Orthoptera is another no less important group in terms of the occurrence of calamities in agricultural communities. Locusts can destroy in a short time vast agricultural tracts, with increased numbers and depletion of their usual food base - mainly weeds and grasses. A number of locust species (eg *Acrididae*) are serious agricultural pests, many of them polyphagous, causing great damage to crops such as sorghum, sunflower, soybeans, millet, wheat, eucalyptus, banana, corn, rice, palms, citrus fruits, sunflower, potatoes, tobacco, sugar cane, beans, etc. (Le Gall et al. 2019) Representatives such as *Calliptamus italicus* (Linnaeus, 1758), *Anacridium melanorhodon* (Walker, 1870), *Schistocerca* sp., *Docioastaurus maroccanus* (Thunberg, 1815), *Australris guttulosa* (Walker, 1870), *Nomadacris septemfasciata* (Serville, 1883), *Locusta migratoria migratoria* (Linnaeus, 1758), *Locusta migratoria migratorioides* (Reiche and Fairmaire, 1849), *Oedaleus* spp. are very important in terms of their interactions with livestock grazing practices.

Most locusts also originate from pastures; grassland ecosystems are subject to agricultural expansion, urbanization, energy development and desertification, making them among the most endangered biomes on Earth (Hoekstra et al. 2005). For some grassland ecosystems and food plantations, the Moroccan grasshopper *Docioastaurus maroccanus* (Thunberg, 1815) or the red grasshopper *Nomadacris septemfasciata* (Audinet-Serville, 1883), this increase in anthropogenic change, together with modern control practices, has led to a reduction in outbreaks (Le Gall et al. 2019).

The current article summarizes species of both orders (Blattodea and Orthoptera) and the corresponding immune responses that are known in them, which is pertinent to the elucidation of the defense mechanisms and would facilitate a number of researchers in the field of biological control of insect pests. Significant species of cockroaches, termites, locusts, and crickets have been analyzed in more details.

**Studies on the defense mechanisms of significant species of Blattodea and Orthoptera**

**Periplaneta americana**

*P. americana* is a species intensively studied for its immune mechanisms due to its importance as a carrier of a number of infectious diseases. Along with several other species, they are vectors of a number of pathogens (32 species of bacteria, including *Salmonella* and *Shigella* species, 15 species of fungi and molds, 7 helminths - intestinal parasites, 2 protozoa and 1 virus that are harmful to humans are carried in or on cockroaches and in their faeces (Mille & Peters 2004, Zarchi & Vatani 2009, Allotey et al. 2009, Akbari et al. 2015). Two species of cockroaches (*B. germanica* and *Eublaberus posticus*) have been studied in cultivation-based studies (Tachbele et al. 2006, Vahabi et
al. 2007). Due to their significance as pests, studies on their immunity have justifiably been intensified. In a study of cockroach hemocytes, Scharrer (1972) reported that they contained a class of unusual cytoplasmic inclusion bodies which seem to undergo striking transformations in response to specific functional demands. Also noteworthy is that the capacity for the uptake of small particles by micropinocytosis is demonstrated by the localization of horseradish peroxidase activity at the cellular surface and within cytoplasmic vesicles. The author concluded that the diversity of structural appearances reflected a division of labor, while the many transitional features of hemocyte morphology favored the concept of functional flexibility of one basic cell type rather than a strict classification into distinctly separate cellular types.

When injecting a specific bee toxin, Karp & Rheins (1980) found a secondary immune response and that this humoral response of cockroaches to soluble protein toxins was specific and had the characteristics of immunological memory. Although insects have a simpler anatomy than vertebrates, the underlying molecular genetics may be as complex. In addition, vertebrate and invertebrate animals may be subject to equally complex, though different, environmental stresses (Karp 1990).

Baines & Downer (1994) investigated the effects of 5-hydroxytryptamine, octopamine and dopamine on phagocytic activity and hemocyte nodule formation in cockroaches. Survival of cockroaches exposed to LD<sub>30</sub> Staphylococcus aureus is increased in the presence of 5-HT and octopamine, while dopamine has no effect. Antagonistic and agonistic studies of cockroach survival support in vitro results, suggesting that both octopamine and 5-HT-sensitive receptors are found in cockroach hemocytes and are involved in the recovery of cockroaches from bacterial infection. Studies of hemocoele and hemocytes in treated cockroaches have shown at least two mechanisms by which 5-HT and octopamine can increase survival are by increasing phagocytosis and nodule formation. Shaban et al. (2010) investigated the cellular and humoral immune responses of adult American cockroaches, P. americana to the Egyptian entomopathogenic nematode Steinernema sp. Nematode injection reduced the total hemocyte count by 12 hours after injection, followed by an increase to the control level at 24 hours after injection. Phenoloxidase (PO) activity in the plasma of cockroaches injected with nematodes increased significantly at 12 hours post-injection, followed by a decrease at 24 hours post-injection. Both activities were significantly higher than those found in non-injected and water-injected P. americana plasma. The results suggest that the bacterial complex Steinernema has effective immunosuppressive mechanisms, leading to septicemia and rapid death of the American cockroach. Mudoi et al. (2020) examined hemocytes in fungal infection with Beauveria bassiana, identifying changes in the dynamics of the groups of prohemocytes (PRs), plasma cells (PLs), granulocytes (GRs) and spherulocytes (SPs), their morphology. GRs, predominant hemocytes involved in cell-mediated defense, responded to infection in different ways, including the formation of fine pseudopodia-like cytoplasmic extensions that accumulate together. Duarte et al. (2020) found that various stressful conditions such as starvation and dehydration do not affect the total number of hemocytes, but there are changes in their number depending on the type. In insects without food and water, the proportion of prohemocytes increases and plasma cells decrease.
Table 1. Classification of different types of immune responses and pathways.

| Classification       | Specification of the immune responses                                                                 |
|----------------------|--------------------------------------------------------------------------------------------------------|
| AMPs                 | Antimicrobial peptides: drosocin, diptericin and others                                                 |
| Signaling            | Mechanisms, relating to immune signaling: IMD, Toll and JAK/STAT                                        |
|                      | The IMD pathway includes the proteins: Imd, Relish, RING, BIR and others                               |
|                      | The Toll pathway includes: Toll, Pelle, Spätzle, Tube, Cactus, Dorsal, DIF and others                  |
|                      | The JAK/STAT pathway includes: JAK, STAT, DOME, Domeless, Hopscotch and others                         |
| Pathogen recognition| PGRPs (peptidoglycan recognition proteins), β-1,3-glucan recognition proteins, immunolectins, integrins|
| Hemocytes            | Lamellocytes, proleukocytes, plasmatocytes and others                                                  |
| Immune responses     | Phagocytosis, nodulation, melanisation, and encapsulation                                              |
| Antiviral responses  | RNA interference: the enzymes Argonaute, R2D2, Dicer and others                                        |

Table 2. List of cockroaches, termites and orthopterans, authors who have investigated their immunity, and studied topics (according to Table 1).

| Blattodea                        | Studied topics (Authors)                                                                 |
|----------------------------------|----------------------------------------------------------------------------------------|
| Archimandrita tessellata         | Hemocytes (Kolundžić et al. 2018)                                                      |
| Blaberus craniifer               | Immune responses (Dularay & Lackie 1987); Hemocytes (Kolundžić et al. 2018)            |
| B. discoidalis                   | Hemocytes, Signaling (Durrant et al. 1993); Signaling (Chen et al. 1995); Signaling (Chen et al. 1999) |
| B. giganteus                     | Hemocytes (Arnold & Salkeld 1967)                                                      |
| Blatta orientalis                | Immune responses (Dularay & Lackie 1987); Hemocytes, Immune responses (Karp 1990)       |
| Blattella germanica              | Hemocytes (Chiang et al. 1988); Signaling (Zhang & Chen 2014); AMPs, Signaling (Zhou et al. 2014); Hemocytes, Immune responses (Lopez-Urbe et al. 2016); AMPs, Signaling (Harrison et al. 2018); AMPs (Silva et al. 2020); Immune responses (Ray et al. 2020); Immune responses (Pan et al. 2020) |
| Byrsotria fumigata               | Hemocytes (Scharrer 1972)                                                               |
| Coptotermes formosanus           | Immune responses (Hussain & Wen 2012); AMPs, Signaling (Husseneder & Simms 2014)         |
| Diploptera punctata              | Hemocytes (Arnold 1970)                                                                |
| Drepanotermes rubriceps          | AMPs (Bulmer & Crozier 2004)                                                           |
| Gromphadorhina coquereliana      | Hemocytes (Lubawy & Słocińska 2020)                                                     |
| G. portentosa                    | Hemocytes (Scharrer 1972); Hemocytes (Gupta 1985); Immune responses (Bronstein & Conner 1984); Hemocytes (Grebtsova & Prisny 2014) |
| Nasutitermes comatus             | AMPs (Bulmer & Crozier 2004)                                                           |
| N. dixoni                        | AMPs (Bulmer & Crozier 2004)                                                            |
| N. fumigatus                     | AMPs (Bulmer & Crozier 2004)                                                            |
| N. exitiosus                     | AMPs (Bulmer & Crozier 2004)                                                            |
| N. graveolus                     | AMPs (Bulmer & Crozier 2004)                                                            |
| N. longipennis                   | AMPs (Bulmer & Crozier 2004)                                                            |
| N. magnus                        | AMPs (Bulmer & Crozier 2004)                                                            |
| N. pluvialis                     | AMPs (Bulmer & Crozier 2004)                                                            |
| N. triodae                       | AMPs (Bulmer & Crozier 2004)                                                            |
| N. walkeri                       | AMPs (Bulmer & Crozier 2004)                                                            |
| Periplaneta americana            | Hemocytes (Scharrer 1972); Hemocytes, Signaling (Lackie 1979); Immune responses, AMPs (Karp & Rheins 1980); Hemocytes (Jones & Bell 1982); |
Hemocytes, Immune responses (Lackie et al. 1985); Immune responses (Dularay & Lackie 1987); Hemocytes, Immune responses (Karp 1990); Signaling, Immune responses (Tunaz & Stanley 2000); Immune responses (Hartman & Karp 1989); Immune responses (Faulhaber & Karp 1992); Signaling, Immune responses (Baines et al. 1992); Signaling, Immune responses (Baines & Downer 1994); Immune responses (Brown et al. 1994); Immune responses (Gritsai et al. 2004); Immune responses (Shaban et al. 2010); Hemocytes, Immune Responses (Mudoi et al. 2020); Immune responses (Duarte et al. 2020)

| Pseudacanthotermes spiniger | AMPs (Lamberty et al. 2001) |
|-----------------------------|-----------------------------|
| Reticulitermes chinensis    | AMPs, Immune responses (Liu et al. 2015) |
| *R. flavipes*               | Immune responses (Chouvenca et al. 2009; AMPs, Immune responses (Zeng et al. 2014)); AMPs (Zeng et al. 2016); AMPs, Hemocytes (Zeng et al. 2018); AMPs, Signaling (Hamilton & Bulmer 2012) |
| *R. speratus*               | AMPs, Signaling (Mitaka et al. 2017) |
| Salganea esakii             | AMPs, Immune responses (Araújo et al. 2021) |
| *S. taiwanensis*            | AMPs, Immune responses (Araújo et al. 2021) |
| Tumulitermes pastinator     | AMPs (Bulmer & Crozier 2004) |

**Orthoptera**

| Acheta domesticus          | Hemocytes (Zhang & Zhang 2021) |
|----------------------------|---------------------------------|
| Aiolopus thalassinus tamulus | Hemocytes (Zhang & Zhang 2021) |
| Allonemobius socius         | Immune responses (Fedorka et al. 2013) |
| Atractomorpha sinensis      | Hemocytes (Zhang & Zhang 2021) |
| Aularches miliaris          | Hemocytes (Zhang & Zhang 2021) |
| Bryodema gebleri           | Hemocytes (Zhang & Zhang 2021) |
| B. gebleri mongolicum      | Hemocytes (Zhang & Zhang 2021) |
| B. nigroptera              | Hemocytes (Zhang & Zhang 2021) |
| Bryodemella tuberculatum dilatum | Hemocytes (Zhang & Zhang 2021) |
| Calliptamus abbreviatus     | Hemocytes (Zhang & Zhang 2021) |
| C. barbarus                | Hemocytes (Zhang & Zhang 2021) |
| C. italicus                | Hemocytes (He et al. 2017); Hemocytes (Zhang & Zhang 2021) |
| Camnula pellucida           | Immune responses (Carruthers et al. 1992) |
| Ceracris fasciata          | Hemocytes (Zhang & Zhang 2021) |
| C. nigricornis laeta        | Hemocytes (Zhang & Zhang 2021) |
| Chondracris rosea          | Hemocytes (Zhang & Zhang 2021) |
| Choroedocus violaceipes    | Hemocytes (Zhang & Zhang 2021) |
| Chorthippus biguttulus      | Immune responses (Kurtz et al. 2002) |
| Dasyhippus barbipes        | Hemocytes (Zhang & Zhang 2021) |
| D. peipingensis            | Hemocytes (Zhang & Zhang 2021) |
| Diabolocatantops pinguis   | Hemocytes (Zhang & Zhang 2021) |
| Decticus verrucivorus      | Hemocytes (Öztürk et al. 2018) |
| Dociostaurus maroccanus     | Signaling (Rafiei et al. 2018) |
| Eupholidoptera smyrnensis   | Hemocytes (Öztürk et al. 2018) |
| Gastrimargus marmoratus     | Hemocytes (Zhang & Zhang 2021) |
| Gesonula punctifrons        | Hemocytes (Zhang & Zhang 2021) |
| Gryllodes sigillatus        | Immune responses (Gershman et al. 2010) |
| Gryllotalpa orientalis      | AMPs, Signaling (Kwon et al. 2014) |
| Insect Species                  | Immune Responses/Signaling | References |
|--------------------------------|---------------------------|------------|
| *Gryllus assimilis*            |                           | (Miller et al. 1999) |
| *G. bimaculatus*               | Immune responses; Immune responses | (Louis et al. 1986); (Rantala & Roff 2005); (Cho & Cho 2019) |
| *G. campestris*                | Immune responses          | (Jacot et al. 2005) |
| *G. firmus*                    | Signaling, Immune responses | (Park & Stanley 2006) |
| *G. texensis*                  | Immune responses; Immune responses | (Adamo et al. 2001); (Adamo 2004); (Shoemaker et al. 2006a); (Shoemaker et al. 2006b); (Adamo & Parsons 2006) |
| *G. veletis*                   | Immune responses          | (Ferguson et al. 2016) |
| *Glyphotmethis* spp.           | Hemocytes                | (Öztürk et al. 2018) |
| *Haplotrupes brunncriana*      | Hemocytes                | (Zhang & Zhang 2021) |
| *Hieroglyphus tonkinensis*     | Hemocytes                | (Zhang & Zhang 2021) |
| *Locusta migratoria*           | Signaling, Immune responses; AMPs; Hemocytes | (Hoffmann et al. 1970); (Hoffmann 1980); (Brehélin et al. 1975); (Brehélin et al. 1991); (Zachary & Hoffmann 1984); (Drif & Brehélin 1994); (Cherqui et al. 1998); (Söderhäll & Cerenius 1998); (Goldsworthy & Söderhäll 2002); (Simonet et al. 2002); (Ouedraogo et al. 2003); (Macours et al. 2003); (Lv et al. 2016); (Duressa & Huybrechts 2016); (Duressa 2015); (Han et al. 2017); (Huybrechts & Coltura 2018); (Yu et al. 2016); (Zheng & Xia 2012); (Jiang et al. 2020); (Zhang & Zhang 2021) |
| *Melanoplus sanguinipes*       | Immune responses          | (Inglis et al. 1996) |
| *Oedaleus asiaticus*           | AMPs, Immune responses    | (Huang et al. 2020) |
| *O. infernalis*                | Hemocytes                | (Zhang & Zhang 2021) |
| *Oxya chinensis*               | Hemocytes                | (Zhang & Zhang 2021) |
| *Paracryptera microptera*      | Hemocytes                | (Zhang & Zhang 2021) |
| *Patanga japonica*             | Hemocytes                | (Zhang & Zhang 2021) |
| *Phlaeoba antennata*           | Hemocytes                | (Zhang & Zhang 2021) |
| *P. infumata*                  | Hemocytes                | (Zhang & Zhang 2021) |
| *Poekilocerus pictus*          | Hemocytes                | (Jain & Ahi 2016) |
| *Pseudotmethis rubimarginis*   | Hemocytes                | (Zhang & Zhang 2021) |
| *Schistocerca gregaria*        | Pathogen recognition, Hemocytes | (Lackie 1979); (Lackie et al. 1985); (Gillespie et al. 2000); (Xia et al. 2000); (Bundey et al. 2003); (Simonet et al. 2005); (Tounou et al. 2008); (Elliot et al. 2002); (Elliot et al. 2003) |
| *Stenocatantops splendens*     | Hemocytes                | (Zhang & Zhang 2021) |
| *Stethophyma grossum*          | Hemocytes                | (Zhang & Zhang 2021) |
| *Teleogryllus commodus*        | Signaling                | (Stanley-Samuelson et al. 1987); (Stanley 2000) |
| *T. oceanicus*                 | Immune responses          | (Simmons 2005) |
| *Trilophidia annulata*         | Hemocytes                | (Zhang & Zhang 2021) |
| *Xenocatantops brachycerus*    | Hemocytes                | (Zhang & Zhang 2021) |
| *X. humilis*                   | Hemocytes                | (Zhang & Zhang 2021) |
| *Zootermopsis nevadensis*      | Hemocytes                | (Lopez-Uribe et al. 2016) |
The German cockroach, *B. germanica*, is a global pest that invades buildings, including homes, restaurants and hospitals, often maintained in unsanitary conditions. As a carrier of diseases and a producer of allergens, this species has major health and economic impact on humans.

Factors contributing to the success of the German cockroach include its resistance to a wide range of insecticides, immunity to many pathogens and its ability, as an extremely universal omnivore, to survive on most food sources. *B. germanica* is a pest of public health worldwide that is difficult to control due to its strong reproductive capacity, adaptability and resistance to insecticides. A recently published genome shows that *B. germanica* has an extremely large number of genes encoding proteins (Harrison et al. 2018). Zhou et al. (2014) annotated and classified functionally in terms of BLAST, GO and KEGG, the genes putatively coding detoxification enzyme systems, insecticide targets, key components in systematic RNA interference, immunity and chemoreception pathways.

López-Uribe et al. (2016) in their study concluded that social insect species have developed behavioral immune defenses that reduce the risk of disease within the group, leading to lower immunity at the individual level. They suggest that insects living in large societies may rely more on behavioral mechanisms, such as hygiene behavior, than on immune function, to reduce the risk of disease transmission in breeding sites among emerging individuals. A significant negative effect on colony size on encapsulation response in individuals was found.

In a study by Harrison et al. (2018), the functions of the 93 significantly expanded gene families were studied in order to explain the successful development of *B. germanica* as a major pest despite adverse conditions. Large extensions have been found in gene families with functions related to the detoxification of insecticides and allelochemicals, protection against pathogens, digestion, sensory perception and gene regulation. This increase may allow *B. germanica* to develop multiple mechanisms of resistance to insecticides and pathogens, and allow for a broad, flexible diet, thus explaining its success in conditions of poor hygiene and repetitive chemical control. Silva et al. (2020) examining the German cockroach found that its defense systems require it to adapt to an unhealthy environment with an abundance of pathogenic microbes, in addition to the potential control of its symbiotic systems. To deal with this situation, four families of antimicrobial genes (defensins, termicins, drosomycins, and attacins) were expanded in its genome. Remarkably, a new family of genes (blatelicins) has recently emerged following the duplication and rapid evolution of the attacin gene, which now encodes a larger proteins with a long range of glutamines and glutamic acids. Screening for AMP gene expression in available transcriptional SR projects of *B. germanica* has shown that while some AMPs are expressed during almost all development, others are limited to shorter periods. Pan et al. (2020) highlighted new directions in the control of *B. germanica*, such as suppressing the cockroach population with *Wolbachia* or paratransgens and combining fungal insecticides with synergistic agents to increase insecticidal efficacy.

Order Blattodea also includes termites. Data show that various immune processes have been identified in 17 species of their representatives, e.g. production of antimicrobial peptides, hemocyte activities, immune responses, signaling [Table 2].

Among Orthopteran species, most insect immunity studies have been performed on migratory locusts. Simonet et al. (2002) have cloned two serine protease inhibitor precursors in this species, contributing to the study of its immune signaling. Goldsworthy et
al. (2003) demonstrated pathogen recognition via β-1,3 glucans as an early step in signaling, as opposed to virtually zero recognition of lipopolysaccharide (LPS) by the locust immune system. Similar findings have been demonstrated by Zheng & Xia (2012), which showed through RNA interference (RNAi) that β-1,3 glucan recognition protein (βGRP) is essential for resistance against fungal pathogens and opportunistic infections with insect gut symbionts.

**Locusta migratoria**

Antifungal immunity in *L. migratoria* is supplemented by a response known as “behavioral fever” whereby insects upregulate their body temperature in order to reduce their infection by a fungus, *Metarhizium anisopliae* (Ouedraogo et al. 2003). Antimicrobial peptides (AMPs) are the typical effectors of the insect immune system. A complete AMP transcriptome analysis of *L. migratoria* is lacking; nevertheless, Lv et al. (2016) have elucidated CSαβ defensins and defensin-like peptides in this species. Huybrechts & Coltura (2018) have pinpointed a role for angiotensin-converting enzyme (ACE) and ACE-inhibitors in fine-tuning the insect immune system by producing complementary AMPs. In a large-scale study on insect hemocytes, Zhang & Zhang (2021) have described hemocyte variations in 35 locust species, including *L. migratoria*. Other Orthopteran species which are objects of insect immunity studies include, notably, the desert locust *Schistocerca gregaria* (Forsskål, 1775) and the house cricket *Acheta domesticus* (Linnaeus, 1758).

**Schistocerca gregaria**

The desert locust, *S. gregaria*, has been investigated to a greater depth in its role as a pest and potential target for biological control. Early on, Lackie et al. (1985) elucidated hemocyte profiles and encapsulation responses. Gillespie et al. (2000) have pinpointed the susceptibility of *S. gregaria* to fungal infection by *Metarhizium anisopliae*. While desert locusts also exhibit the protective response known as “behavioral fever”, Bundey et al. (2003) demonstrated that it’s an integral part of the insect’s immune system by showing that it can be suppressed by the corticosteroid dexamethasone. Tounou et al. (2008) demonstrated that the microsporidium *Nosema (Paranosema) locustae* Canning, 1953 is an efficient control agent for *S. gregaria* populations, limiting the number of individuals that reach adulthood and discovered mostly synergistic effects during co-infection of *S. gregaria* with *M. anisopliae*. While Simonet et al. (2005) reported the expression of pacifastin-like peptide precursors in desert locusts, surprisingly little is known about the transcriptome of *S. gregaria* under conditions of stress and infection and the effectors of its immune system. Together with an apparent lack of studies of locust immunity against viral pathogens, this represents a large gap in the current knowledge of immunity in this species. It is projected that, due to the significant role of *S. gregaria* as pest in Sub-Saharan Africa, its role in future studies of insect immunity will increase.

**Acheta domesticus**

The house cricket *A. domesticus* is popular among insect breeders around the world specifically due to its high nutritional value and suitability as food source for amphibian and reptilian exotic pets. Nevertheless, its prevalence as live food source has been declining recently due to its susceptibility to the Cricket Paralysis Virus (CrPV), which causes 95% mortality in infected cricket species (Plus & Scotti, 1984). Early research with crickets focused on pathogen-induced behavioural fever (Adamo 1998). Ardia et al. (2012) have found tradeoffs between induced
immune responses in *A. domesticus* and metabolic rate/antimicrobial activity. Sorrell & Killian (2020) investigated the influence of RNA interference (RNAi) of the fragile X mental retardation gene in house crickets, concluding that its deletion damages the immune system in male, but not female crickets. Reginald et al. (2021) studied the immune responses of *A. domesticus* to injections of pathogenic *Escherichia coli* K1 bacteria, elucidating signaling via prophenoloxidase (ProPO) and responses, associated with hemocyte biogenesis. Overall, *A. domesticus* has served as a model organism in some insect immunity studies, but research has been sporadic, with little systematic understanding of this species immune system, especially in response to fungal and viral pathogens.

**Conclusion**

Both orders of insects belong to the group of hemimetabolan insects and although they differ from a biological and ecological point of view, they are important for their role as vectors of a number of infectious diseases (Blattodea) as well as enemies with significant economic importance in the field of agriculture (Orthoptera). In this regard, the study of the defense mechanisms of these insects is important for a more in-depth study of the possibilities of control when their population density is high. The processes of innate immunity established so far (hemocytes activities, antimicrobial peptides, pathogen recognition, signaling pathways, immune and antiviral responses) are important and reveal new data and facts, which would lead to gaps in knowledge regarding the effects of various groups of pathogens on them and the registered insect physiological protective responses.

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