Biological control of locusts and grasshoppers: A review

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Abstract

Locusts and grasshoppers (Orthoptera: Acrididae) are pests of agricultural importance, devastating crops and pastures. This group includes hundreds of pest species and affects the livelihoods of one in every ten people worldwide. Their outbreaks can be chronic or episodic, with alternating periods of invasion and recession. Here, we review the natural enemies of locusts and grasshoppers in both their native and invaded ranges across the globe to assess the need for their conservation and maintenance as part of the natural suppression of outbreaks and to augment outbreak suppression as potential biological control agents. More than 70 natural enemies have been reported to attack locusts and grasshoppers, including entomopathogenic fungi, bacteria, nematodes, predatory insects, birds, reptiles, and mammals. Particular attention is given to the well-studied species of locusts and grasshoppers for which more information is available and to natural enemies in the locust-affected countries as part of the recent trend of looking for indigenous natural enemies. Such organisms can play a vital role in integrated pest management strategies for locusts and grasshoppers, particularly entomopathogens that can be incorporated with chemical pesticides into the management system. Among the organisms considered, *Metarhizium acridum* is noteworthy for inclusion in integrated pest management programs.

Keywords

Agricultural pests, entomopathogens, integrated pest management, invasion, natural enemies, recession

Introduction

Locusts and grasshoppers (L&G) are among the voracious insect pests belonging to the family Acrididae and mostly live in dry grassland and desert areas. Their economic importance is well established (Lomer et al. 2001, Song et al. 2018, Zhang et al. 2019). The family comprises about 10,000 species in the suborder Caelifera and includes many potential pests of field crops, gardens, pastures, and forests (Usmani and Usmani 2018). L&G are polyphagous and profoundly different from other pests because of their rapid population increase to catastrophic levels, and the nymphal stages of some species congregate to form dense bands that have the potential to cause substantial losses in a very short time (Peng et al. 2020, Qayyum et al. 2024). The winged adults transform into swarms that can migrate over long distances of as much as hundreds of kilometers in a single day, invading previously uninfested regions and rapidly destroying vegetation and crops, resulting in major socio-economic losses on an international scale (Zhang et al. 2019). L&G outbreaks destroy the food sources of humans, animals, and wildlife, thus affecting food security and biodiversity. Losses due to these pests are not limited to damage to green vegetation; the resulting loss of vegetation cover results in increased runoff and soil erosion (Latchininsky 2008). From 2018 to 2020, Africa, the Middle East, and Southeast Asia experienced one of the most severe outbreaks of the desert locust, *Schistocerca gregaria* (Forskål, 1775 (Orthoptera: Acrididae). In 2018, an outbreak began in the Arabian Peninsula with the first swarms seen in early 2019 and subsequently increasing and spreading by the end of the year to cover an area from the Horn of Africa to India/Pakistan, including Eritrea, Ethiopia, Kenya, Somalia, Saudi Arabia, Egypt, Yemen, Oman, Iran, Pakistan, and India (FAO 2020, World Bank 2020).

Most L&G control programs still revolve around treatments based on conventional chemical pesticides, including malathion, lambda-cyhalothrin, fipronil, etc. Injudicious use of these chemical pesticides has elicited many serious concerns related to the impact on human health, aquatic and terrestrial life, biodiversity loss, and hazards to environmentally sensitive areas such as waterways, national parks, inhabited areas, and so on (Henschel 2015). The harmful effects of chemical pesticides have led researchers toward eco-friendly management tactics, including biological control as an important component of integrated pest management with a range of other management actions (Hunter 2004, Magor et al. 2008, Shi et al. 2019, Dakhel et al. 2020). The entomopathogens, together with predators, parasites, and parasitoids of locusts and grasshoppers, play a key role in regulating locust populations at low densities with minimum loss to biodiversity and fewer negative effects on human and animal health. Microbial control offers a reliable pest control method using entomopathogenic microorganisms, including fungi, bacteria, viruses, protozoa, nematodes, and microsporidia, which are derived from the natural environment and usually exhibit a significant degree of host specificity (Halouane et al. 2013). Globally, entomopathogens are used against a variety of insect pests with great advantage and success (St-Leger et al. 2009). Nowadays, fungal-based biopesticides are receiving substantial recognition in the control of L&G worldwide (Mullié and Guèye 2009, Sharma and Sharma 2021, Owuor and McRae 2022). They are considered very selective and have no negative impact on non-target species. Birds, amphibians, and reptiles do not leave sprayed areas, nor do they become intoxicated by the effects of the fungal-based biopesticides, and their populations often temporarily increase (Mullié 2007). This could be attributed to the fact that fungal-infected insects become sluggish and easy prey for birds. Thus, *Metarhizium acridum* (Hypocreales: Clavicipitaceae) enhances the impact of birds, and entomopathogens give evidence of synergetic effects in the case of birds (Mullié et al. 2021). Additionally, their integration with other control methods can be helpful in prolonging the effectiveness of control, as some entomopathogens, such as *Paranosema locustae* (Microsporidia), can become established within the host population (Zhang et al. 1995, Lange et al. 2020).

On the other hand, L&G are also known to be important to the food web of various organisms, especially small mammals (e.g., ground squirrels, shrews, and mice) (Churchfield et al. 1991, Russell and Detling 2003), birds (e.g., seagulls), and other insects (Dysart 1996). Since small mammals reproduce quickly and require large quantities of prey to fuel a rapid metabolism, they can be an excellent resource for limiting L&G populations (Churchfield et al. 1991). Consequently, the population of L&G can be regulated by natural enemies, particularly microbes, birds, and insects, keeping populations at low densities as part of maintaining a balanced ecosystem. If a population of natural enemies is removed from a particular ecosystem by any means (e.g., by non-selective insecticides), the L&G population has an increased chance of outbreaks, and once the L&G population increases, natural enemies are less effective in limiting their population. Here, we summarize the biocontrol agents associated with L&G by considering their potential in the integrated management of developing biological control strategies. Many studies on this subject have been conducted because of the importance of L&G pests.

Microbial control of locusts and grasshoppers

Entomopathogenic fungi (EPF).—A comprehensive list of entomopathogenic fungi (EPF) collected from L&G is given in Table 1. Some of these entomopathogenic fungi have proven to be the most common and effective means of biological control of L&G populations, either through augmentative control of outbreaks or by inducing epizootics in L&G populations. Their mode of action contributes to their success in that, unlike other microorganisms, EPF do not need to be ingested and usually infect their host by direct contact with the host cuticle and penetrating the haemocoel through hyphal body penetration (Butt and Goettel 2000). The host can be infected in several ways, i.e., through direct contact during spray application, subsequent pick-up from treated vegetation, horizontal transmission (a disease caused by infected to healthy insects), and vertical transmission (disease transmission through parents to offspring via transovarial or transovum transmission) (Kreutz et al. 2004, Zimmerman 2007, Jay et al. 2019). In the case of acridids, horizontal transmission does not happen regularly because of the requirement for very high humidity around the fungus-killed cadaver for several days. External sporulation among acridids is rare given their typical environment or due to contact with enough conidia contaminating the soil or phylloplane habitat of the insect. EPF are safer than chemical pesticides because of several biological traits, including host specificity, high reproductive rate and long-term survival, multiple infection cycles, and short generation time. These characteristics provide EPF with good potential as biocontrol agents against L&G (Sharma and Sharma 2021). Importantly, EPF-infected insects show sublethal effects, such as feeding cessation (Tefera and Pringle 2003) and reduced reproduction and survival potential of progeny (Dembilio et al. 2010, Wakil et al. 2022).

Currently, *M. acridum* is well known as a microbial control agent for L&G (Prior and Greathead 1989, Milner 2000, Aw and Hue 2017). Fungi of the genus *Metarhizium* are often the first choice among microbial control agents for inundative control. Moreover, molecular and biochemical analyzes have shown its wide distribution patterns ranging from the Arctic to the tropics and that it can colonize an impressive array of environments, including forests, savannahs, swamps, coastal zones, and deserts (Bidochka and Small 2005, Abro et al. 2019). US Environmental Protection Agency standards indicate that *M. anisopliae* has no impact on humans or other mammals in the field (Siegel 1997, Ahirwar and Singh 2023). Australia and China are successfully using entomopathogens against locusts and grasshoppers. About 15% of all locust control by the Australian Plague Locust Commission is done using *M. acridum*. In China, over 100,000 ha are sprayed with *M. acridum* and *Paranosema locustae* (Microsporidia) every year (Zhang et al. 2019). *M. acridum* is also used regularly as a control agent against locusts in Mexico (Poot-Pech et al. 2018) and was used to treat large areas (>100,000 ha) infested with desert locusts in Eastern Africa from 2020 to 2021 (Owuor and McRae 2022).

Microsporidia.—A comprehensive list of microsporidia collected from locusts and grasshoppers is given in Table 1. One particular microsporidian, *P. locustae* (Microsporidia), was the first microbial control agent developed for L&G control; previously, it was known as *Nosema locustae* and *Antonospora locustae* (Johnson 1997, Slamovits et al. 2004). In the early 1980s, *P. locustae* was developed as a biological control agent for L&G (Zhang and Lecoq 2021). More than 120 grasshopper species are susceptible to this pathogen (Lange 2005, Murray 2016). *P. locustae*, as an obligate parasite, reproduces in host target cells. Its infection involves the polar tube of the spore injecting its plasma into the target cells, causing high mortality in L&G. The pathogen's main target organ is the host's adipose tissue (fat body). *P. locustae* penetrates into the fat bodies of cells and produces meronts, sporonts, sporoblasts, and spores (Canning 1962, Solter et al. 2012). The pathogens' high capacity to sporulate in infected hosts, vertical disease transmission, and wider host range within the orthopteran insect order make them potential microbial control agents for L&G control in deserts and grasslands (Shi et al. 2009, 2018, 2019). While it has a broad host spectrum in Orthoptera, *P. locustae* is safer for non-orthopterans, humans, animals, and other non-target organisms (Menapace et al. 1978, Yuan et al. 2020, Zhang and Lecoq 2021).

Entomopathogenic viruses (EPVs).—Entomopathogenic viruses (EPVs) have been isolated from more than 1,000 insect species belonging to 16 families and from at least 13 different insect orders (Raj et al. 2022). They offer several advantages over conventional chemical pesticides, such as safety to non-target organisms, as well as being precise and ecologically stable. A comprehensive list of EPVs collected from locusts and grasshoppers is given in Table 1. The pathogenic potential of viruses has long been recognized, but interest in using viruses in biological insect pest control programs has increased over the last 40 years (Dakhel et al. 2020, Xu et al. 2022). For example, *Entomopoxvirus* B can infect 15 species of locusts and grasshoppers. The EPV of the migratory grasshopper *Melanoplus sanguinipes* (Fabricius, 1798) (Orthoptera: Acrididae) has been extensively investigated, and it can infect two related species: *M. differentialis* and *M. packardii* (Streett and McGuire 1990, Dakhel et al. 2020).

Entomopathogenic bacteria (EPB).—Entomopathogenic bacteria (EPB) are widely used against a wide variety of insect pests, with more than 90 species derived from natural resources (Waterfield and Daborn 2002, Azizoglu et al. 2020, Ali et al. 2022). EPB from the families Enterobacteriaceae, Bacillaceae, Streptococcaceae, Micrococcaceae, and Bacillaceae are insect pathogens. A comprehensive list of EPB collected from locusts and grasshoppers is given in Table 1. *Serratia marcescens* is an obligatory gram-negative bacterium that was originally isolated from the desert locust in Kenya and has proven effective against L&G in laboratories (Tao et al. 2006). Among the available EPB species, *Bacillus thuringiensis* is the most common and widely used against insect pests. This gram-positive bacterium is extracted from plants, soil, and the guts of lepidopterous and coleopterous insects (Schünemann et al. 2014, Kumar et al. 2021). *B. thuringiensis* expresses two main types of protein toxins: crystal (Cry) and cytoplasmic (Cyt) (Kumar et al. 2021). Currently, there are 75 known crystal toxin subtypes that are highly specific to their target insects (Crickmore et al. 2020), and the endotoxin Crystal 7A is lethal against acridids (Song et al. 2008, Wu et al. 2011).

Entomopathogenic nematodes (EPNs).—Entomopathogenic nematodes (EPNs) are internal parasites of L&G and complete their development inside their hosts by feeding on hemolymph and tissue. Their presence can reduce fecundity, sterilize females, and eventually result in host death (Cranshaw 2008, Shairra 2009, Ghimire 2021, Fathy and Abd El-Rahman 2023). EPNs are obligate parasites that kill their hosts with the aid of mutualistic bacteria present in their intestines. They enter the host body through natural openings and release bacteria in the host gut; the bacteria tolerate the insects' cellular and non-cellular activities and inhibit immune responses (Youssef 2008, Fathy et al. 2023). The bacteria then multiply in the haemocoel and cause fatal septicemia (Jung and Kim 2007, Sharma et al. 2019). EPNs complete 2–3 generations in the host body, and infective juveniles come out of the host body to infect new hosts (Park and Kim 2000, Fathy and Abd El-Rahman 2023). A comprehensive list of nematodes collected from L&G is given in Table 1.

Table 1. Literature reports of microbial natural enemies collected from locusts and grasshoppers.

Natural Enemy	Pathogen Sp.	Acridid species	Attacked stage	Location of record	References
Fungi	*Metarhizium acridum*	*Locusta migratoria*	Nymph	China	Liu et al. 2019
		Schistocerca gregaria	Adults	United Kingdom	Bateman et al. 1996
		Hieroglyphus daganensis, Oedaleus senegalensis, Kraussella amabile	Nymph and adult	Africa	Lomer et al. 1997a
		Locustana pardalina	Adults	South Africa	Arthurs and Thomas 2000
		S. gregaria	Adults	United Kingdom	Arthurs and Thomas 2001
		S. gregaria	Nymphs	Africa	Tounou et al. 2008
		S. gregaria	Nymphs	Mauritanie	Etheimine et al. 2013
		S. gregaria	Nymph and adult	Africa	Kamga et al. 2022
		Dociostaurus maroccanus	Adults	Spain	Valverde-Garcia et al. 2018, 2019
		L. migratoria	Adults	Canada	Ouedraogo et al. 2003
		Tropidacris collaris, Cornops frenatum frenatum, Parascopas obesus	Adults	Brazil	Schmidt et al. 2018
		Uvarovistia zebra	Adults	Iran	Mohammadbeigi and Port 2015
		S. gregaria	Nymph	Sudan	Atheimine et al. 2014
		S. gregaria	Adults	United Kingdom	Blanford and Thomas 2001
		S. gregaria	Adults	Niger	Mullié et al. 2021
		S. gregaria	Nymph	Algeria	Milat-Bissaad et al. 2011
		S. gregaria	Nymph	Egypt	Abdelatef et al. 2009
		S. gregaria, Euprepocnemis plorans	Nymph	Egypt	El-Maghraby et al. 2009
		L. migratoria	Adult	China	Zhang and Hunter 2005
		L. migratoria	Adult	China	Jiang et al. 2020
		Patanga succincta	Nymph and adult	Thailand	Samšiňáková and Purrini 1986
		Zonocerus variegatus	Nymph and adult	Africa	Chapman and Page 1979
		S. gregaria	Nymph and adult	Sweden	Gunnarsson 1988
		Poekilocerus pictus	Adult	Bangalore	Ramanujam et al. 2022
		Oedaleus senegalensis	Nymph and adult	Niger	Langewald et al. 1999
		L. migratoria	Nymphs	Russia	Tokarev et al. 2011
		O. senegalensis	Adult	Niger	Blanford et al. 1998
		L. migratoria	Nymph	Madagascar	Welling et al. 1994
		S. gregaria, Hieroglyphus daganensis	Nymph and adult	Mali	Caudwell and Gatehouse 1996
		Z. variegatus	Adults	United Kingdom	Thomas and Jenkins 1997

Natural Enemy	Pathogen Sp.	Acridid species	Attacked stage	Location of record	References
Fungi	*Metarhizium acridum*	*H. daganensis*, *O. senegalensis*, *Kraussella amabile*	Nymph and adult	Africa	Lomer et al. 1997a
		Melanoplus sanguinipes	Nymphs	Canada	Inglis et al. 1997b
		S. gregaria	Adults	France and United Kingdom	Prior et al. 1995
		M. sanguinipes, *L. migratoria*, *S. gregaria*	Adults	Madagascar	Nowierski et al. 1996
		S. gregaria, *Ornithacris cavroisi*	Adult	Africa - Asia	Abraham et al. 1991
	M. flavoviridae	*S. gregaria*	Nymphs	Mauritania	Kooyman and Godonou 1997
		H. daganensis	Nymph and adult	Benin	Lomer et al. 1997a
		P. vittatum	Nymph and adult	Australia	Milner et al. 1994
		L&G	Adult	United Kingdom	Thomas et al. 1995
		H. daganensis, *O. senegalensis*, *K. amabile*	Nymphs	Niger, Mali	Lomer et al. 1997b
		Z. variegatus	Adult	Benin	Lomer et al. 1993
		Ch. terminifera, *P. vittatum*	Nymph	Australia	Milner and Prior 1994
		S. gregaria	Nymphs	Mauritania	Langewald et al. 1997
		S. gregaria	Adults	United Kingdom	Seyoum et al. 1994
		Z. variegatus	Adults	Benin	Thomas et al. 1997
		L. pardalina	Nymphs	South Africa	Price et al. 1997
		R. schistocercoides	Nymph	Brazil	Vicentini and Magalhaes 1996
		S. gregaria	Adult	United State of America	Moore et al. 1992
		P. vittatum	Adults	Australia	Baker et al. 1994
		Z. variegatus	Adults	Benin	Douro-Kpindo et al. 1995
		S. gregaria	Adult	United Kingdom	Bateman et al. 1993
		S. americana	Adult	Africa	Sieglaff et al. 1998
	M. brunneum	*Anabrus simplex*	Nymph	USA	Foster et al. 2011
	M. robertsii	*M. sanguinipes*	Adult	USA	Zembrzuski 2023
	Beauveria bassiana	*M. sanguinipes*	Adult	Canada	Marcandier and Khachatourians 1987
		M. sanguinipes	Adult	Canada	Bidochka 1989
		M. sanguinipes	Adult	Canada	Bidochka and Khachatourians 1990, 1991, 1992
		Grasshoppers	Nymph and adult	Mali	Johnson et al. 1992
		S. gregaria	Adults	United Kingdom	Bateman et al. 1996
		M. sanguinipes	Adult	Canada	Inglis et al. 1997a
		M. sanguinipes	Nymphs	Canada	Inglis et al. 1997b
		S. cancellata	Adults	South America	Pelizza et al. 2020
		M. sanguinipes	Adults	England	Marcandier and Khachatourians 1987
		M. sanguinipes	Nymph	Canada and Africa	Inglis et al. 1996
		Dociostaurus maroccanus	Adults	Spain	Valverde-Garcia et al. 2018
		S. gregaria, *A. simplex*	Nymph and adult	Pakistan	Wakil et al. 2022
			Nymph	USA	Foster et al. 2011
		Dichroplus maculipennis, *Ronderosia bergii*	Nymph	Argentina	Pelizza et al. 2023
		Poekilocerus pictus	Adult	Bangalore	Ramanujam et al. 2022
		S. gregaria	Nymph	Algeria	Milat-Bissaad et al. 2011
		S. gregaria	Nymph	Egypt	Abdelatef et al. 2009
		S. gregaria E. plorans	Nymph	Egypt	El-Maghraby et al. 2009
		Uvarovistia zebra	Adults	Iran	Mohammadbeigi and Port 2015
		L. migratoria, *S. gregaria*	Nymph	Russia	Levchenko et al. 2020
		Crassula pellucida, *Malanoplus* sp.	Adult	USA	MacLeod 1954
		M. sanguinipes	Nymph and adult	USA	Marcandier and Khachatourians 1987
		Trimerotropis pallidipennis, *Dorycera maculipennis*	Nymph	Argentina	Pelizza et al. 2023
		M. sanguinipes	Nymph and adult	Canada	Johnson and Goettel 1993
		Cryptocatantops haemorrhoidalis, *Acrotylus blondeli*, *H. daganensis*	Nymph and adult	Mali	Delgado et al. 1999
		S. gregaria	Nymphs	Benin	Nasseh et al. 1992
		L. migratoria	Adult and nymph	Canada	Wu and Rozlomiy 2021
	B. brongniartii	*L. migratoria*, *S. gregaria*	Nymph	Russia	Levchenko et al. 2020
		M. sanguinipes	Adult	Canada	Khachatourians 1992
	B. cylindrospora	*M. sanguinipes*	Adult	Canada	Khachatourians 1992
	B. densa	*M. sanguinipes*	Adult	Canada	Khachatourians 1992
	Paecilomyces farinosus	*M. sanguinipes*	Adult	Canada	Khachatourians 1992

Natural Enemy	Pathogen Sp.	Acridid species	Attacked stage	Location of record	References
Fungi	*Entomophaga grylli*	*M. sanguinipes*, *M. bivittatus*	Adults	Argentina Alberta, Canada	Erlandson et al. 1988, 2001, Pelizza et al. 2020
		Camnula pellucida	Nymph and adult	USA	Carruthers et al. 1997
		C. pellucida, *Dissosteira carolina*, *L. migratoria*	Nymph and adult	USA	Soper et al. 1983, Ramoska et al. 1988
		M. differentialis, *C. pellucida*	Adult	USA	Ramoska et al. 1988
		Hesperotettix speciosus, *H. viridis*	Adult	USA	McDaniel 1986
		Camnula pellucida	Adult	USA	Sawyer et al. 1997
	Aspergillus parasiticus	*M. sanguinipes*	Adult	USA	Moore and Erlandson 1988
	A. oryzae	*L. migratoria*	Nymph	China	Zhang et al. 2015, You et al. 2023
	Verticilium lecanii	Grasshoppers	Nymph	United Kingdom	Shah and Pell 2003
		M. sanguinipes, *M. bivittatus*, *M. packardii*	Adult	Canada	Johnson et al. 1988
	Verticillium spp.	L&G	Nymph	United Kingdom	Shah and Pell 2003
	Hirsutella spp.	L&G	Nymph	United Kingdom	Shah and Pell 2003
	Entomophthora spp.	*S. gregaria*	Adult nymph	Egypt	Youssef 2014
	Sorosporella sp.	*L. migratoria*	Nymph	Madagascar	Welling and Zimmerman 1997
	Paecilomyces spp.	*L. migratoria*, *S. gregaria*, *M. sanguinipes*	Adult	Madagascar	Nowierski et al. 1996
Microsporidia	*Paranosema locustae*	*S. gregaria*, *E. plorans*	Nymph	Egypt	El-Maghraby et al. 2009
		Grasshoppers	Nymph and adult	Mongolia	Dong 1989
		M. bivittatus	Nymph and adult	USA	Henry and Omar 1974.
		Ceracris kiangsu	Nymph and adult	China	Chen et al. 2002
		Chondracris rosea	Nymph and adult	China	Liu and Chen 1996
		Grasshoppers	Nymph and adult	China	Ma et al. 2005
		Grasshoppers	Nymph and adult	China	Chen et al. 2007
		S. gregaria	Nymph	Africa	Tounou et al. 2008
		S. gregaria, *Oedaleus senegalensis*	Nymph	Africa	Tounou et al. 2011
		S. cancellata	Nymph and adult	USA	Lange et al. 2000
		Agropyron spicatum, *A. smithiia*, *Artemisia frigid*	Nymph	USA	Henry et al. 1973
		L. migratoria	Nymph and adult	West African	Canning 1962
		M. sanguinipes, *M. packardii*, *Camnula pellucida*	Nymph and adult	Canada	Ewen and Mukerji 1980
		L. migraioria, *M. sanguinipes*	Adult	USA	Henry 1969
		Grasshoppers	Nymph	China	Peng et al. 2018
		L. migratoria	Nymph and adult	China	Li et al. 2020
		S. cancellata, *Dichroplus schulzi*, *Ronderosia bergii*	Nymph	Argentina	Pocco et al. 2020
		Grasshoppers	Adult	West Africa	Henry et al. 1985
		L. migratoria	Adult	China	Li et al. 2020
		L. migratoria, *S. gregaria*	Adult	Russia	Tokarev et al. 2022
		L. migratoria	Nymph	Russia	Tokarev et al. 2011
		Grasshoppers	Nymph and adult	USA	Lange et al. 2020
	Nosema acridophagus	*M. sanguinipes*	Adult	USA	Erlandson et al. 1985
		M. bivittatus, *M. differentialis*, *S. americana*	Adult	USA	Henry 1969
	N. Cuneatum	*M. sanguinipes*	Adult	USA	Erlandson et at. 1988
		M. differentialis	Adult	USA	Henry 1971
		M. femurrubrum, *S. americana*	Adult	USA	Henry 1969
	N. acridophagus	*M. sanguinipes*	Adult	USA	Erlandson et al. 1988, Erlandson et al. 2001
		M. bivittatus, *M. differentialis*, *S. americana*	Adult	USA	Henry 1969
	Malameba locustae	*L. pardalina*	Adult	Africa and USA	Prinsloo 1960, Henry 1968
		M. sanguinipes	Adult	Canada	Hinks and Ewen 1986
	N. acridophaga	*M. sanguinipes*	Adults	USA	Boorstein and Ewald 1987
	N. entomophaga,	L&G	Nymph	Argentina	Johnson 1997
	Johenrea locustae	*L. migratoria*	Nymph	Madagascar	Lange et al. 1996
	Perezia dichroplusa	*Dichroplus elongata*	Adult	South America	Lange 1987
	N. acridophagus	*M. bivittatus*	Nymph and adult	USA	Henry and Omar 1974
	N. cureatum	*M. bivittatus*	Nymph and adult	USA	Henry and Omar 1974
Virus	Nuclear Polyhedrosis Virus (NPV)	*S. americana*	Adults	Egypt	Mahmoud and Soliman 2015
		M. sanguinipes, *M. bivittatus*, *M. differentialis*, *S. americana*	Adult	USA	Henry and Jutila 1966

Natural Enemy	Pathogen Sp.	Acridid species	Attacked stage	Location of record	References
Virus	Nuclear Polyhedrosis Virus (NPV)	*L. migratoria, S. gregaria*	Nymph	Israel	Bensimon et al. 1987, Faktor and Raviv 1996
		S. americana	Adult	Egypt	Mahmoud and Soliman 2015
		M. sanguinipes, M. bivittatus, M. differentialis, S. americana	Adult	USA	Henry and Jutila 1966
		L. migratoria, S. gregaria	Nymph	Israel	Bensimon et al. 1987, Faktor and Raviv 1996
	Entomopoxvirus	*M. sanguinipes, Phoetaliotes nebrascensis, Arphia conspersa*	Nymph	USA	Langridge et al. 1983
		Cataloipus fuscocoeruleipes	Nymph and Adult	Yemen	Purrini 1989
		S. gregaria, Chortipes sp.	Nymph and Adult	Africa-Asia	Purrini and Rohde 1988
		L. migratoria	Nymph and Adult	Africa-Asia	Purrini et al. 1988
		Oedaleus senegalensis, O. nigeriens, Kraussaria angulifera, Heteracris annulosus, Spharagemon collare, Xanthippus corallipes, Psoloessa delicatula, Encoptolophus sordidus, P. nebrascensis	Adult	Senegal, USA	Henry et al. 1985
	Small RNA virus	*Melanoplus bivittatus*	Nymph and adult	USA	Jutila et al. 1970
Bacteria	*Malpighamoeba locusta*	*M. differentatialis, M. mexicanus, M. femurrubrum*	Adult	USA	Taylor and King 1937
	Bacillus weihenstephanensis, Pseudomonas aeruginosa	*S. gregaria*	Nymph	Egypt	Mashtoly et al. 2019
	B. cereus	*S. gregaria*	Nymph	Egypt	Reda et al. 2018
	Coccobacillus acridiorum	Grasshoppers	Nymph and adult	Mexico	Lord 2005
	Serratia marcescens	*S. gregaria*	Nymph and adult	UK	Bundey et al. 2003
	B. thuringiensis	L&G	Nymph	Germany	Zelazny et al. 1997
	Rickettsiella grylli	*S. gregaria*	Adult	Africa-Asia	Vago and Martoja 1963
		L. migratoria	Adult	Africa-Asia	Vago and Martoja 1963
		Zonocerus variegatus, M. sanguinipes, M. differentialis	Adult	Senegal	Henry et al. 1986
	R. schistocerc	*S. gregaria, L. migratoria*	Adult	Africa-Asia	Vago and Meynadier 1965
Nematodes	*Hexamermis* sp.	Grasshoppers	Nymph	America	Puttler and Thewke 1971
	Agamermis ecaudate Mermis subnigrescens	L&G	Adult	America	Rees 1973
	M. nigrescens, Gordius robustus	Grasshoppers	Adult	USA	Cranshaw 2008
	Steinernema carpocapsae	*S. gregaria*	Nymph and adult	Egypt	Youssef 2014
	Henlea lefroyi	Locusts	Adult	Thailand	Usmani and Usmani 2018
	M. quirindiensis	*P. vittatum, Praxibulus* sp., *Chortoicetes terminifera*	Nymph and adult	Australia	Baker and Poinar Jr 1986

Arthropods and vertebrates as natural enemies of locusts and grasshoppers

Consideration of the population dynamics of L&G leads to a focus on biological control options using non-microbial control agents, such as arthropods and vertebrates. Up to 70–80% of the first instar stage L&G can die due to inadequate water reserves, cannibalism, and predation by ants. Different ants, parasitic wasps, predatory beetles, reptiles, and birds feed on locust hoppers (Zhang and Hunter 2017, Zhang et al. 2019).

Insects.—Parker and Wakeland (1957) estimated that an average of 19% of L&G egg pods are destroyed by predators and that, at the local level, mortality may be as high as 100%. Acridid egg pods can also be destroyed by the larvae of bee flies, blister beetles, and ground beetles (Parker and Wakeland 1957, Ghoneim 2013). The insects that feed on grasshopper eggs can be divided into two groups—predators and parasitoids—based on the insects' feeding method. Egg predators attack the eggpod as a whole, feeding externally on the grasshopper eggs.

Predators are capable of moving from one egg or eggpod to another as they complete their development. *Anastoechus angustifrons* Paramonov, 1930 (Diptera: Bombyliidae) are predators of grasshopper eggs. The larvae of blister beetles (meloids) are an important group of predators of grasshopper eggs, and while the larvae are predaceous, the adults feed exclusively on vegetation (Ghahari et al. 2009, Shanklin et al. 2010, Ghoneim 2013). Parasitoids feed internally and complete their development within a single egg. In general, parasitoids of the eggs of insects are usually tiny hymenopterous wasps of the family Scelionidae (Baker et al. 1996). The most important genus is *Scelio* (Latreille, 1805) the hymenopterous egg parasitoid with the greatest potential for use as a successful biological control agent (Greathead 1992). Khajehzadeh and Ghazavi (2000) reported that the parasitoid *Scelio flavibarbis* (Marshall, 1874) infests 27% of egg capsules, destroying some 4–16% of the eggs of the migratory locust, while Hunter et al. (1998) reported parasitism rates of as much as 50% of the eggs of the Australian plague locust.

Mites.—One of the important biological checks on grasshopper numbers is the grasshopper mite, *Eutrombidium trigonum*

Table 2. Literature reports of arthropod and vertebrate that are natural enemies of locusts and grasshoppers.

Natural Enemy	Predator species	Acridid species	Attacked stage	Location of record	References
Insects	Meloid beetles, Bombylid flies, *Scelio pembertoni, S. parvicornis*	Grasshoppers	Eggs	Africa	Greathead 1992, Dysart 1996
	S. flavibarbis	L&G	Eggs	North America	Ghahari et al. 2009
	Hylemya cilirura	Locusts	Nymph	Pakistan	Usmani and Usmani 2018
	Acridomyia canadensis	Grasshoppers	Adult	Canada	Rees 1973
	Hylemya angustifrons	Grasshoppers	Eggs	Canada	Hostetter 1994
	Neorhynchocephalus sackenii	Grasshoppers	Nymph and adult	North American	Prescott 1960, Smith 1958
	Mantis religiosa	Grasshoppers	Nymph	British Columbia	Cannings 2007
	Pterostichus gebleri	Grasshoppers	Nymph and adult	China	Shi et al. 2018
	Telenomus sp.	L&G	Eggs	China	Ji et al. 2008
	Blaesoxipha pachytyli, Trichopsidea ostracea	Locusts	Eggs and nymph	Australia	Baker 1995
	Scelio spp.	L&G	Egg	Australia	Baker et al. 1996
Spiders	*Phiddipus audax*	Grasshoppers	Nymph and adult	USA	Maloney et al. 2003
	Pardosa monticola	Grasshoppers	Nymph	UK	Cherrill and Begon 1989
	Xysticus cristatus	Grasshoppers	Nymph	British	Richards and Waloff 1954
	Lycosidae spiders	Grasshoppers	Adult		Oedekoven and Joern 2000
	Rabidosa rabida	Grasshoppers	Nymph and adult	USA	Maloney et al. 2003
	Agelena labyrinthica	Grasshoppers	Adult	USA	Young and Edwards 1990
	Trochosa parthenus	Grasshoppers	Adult	USA	Punzo and Kukoyi 1997
Mites	*Eutrombidium locustarum*	Grasshoppers	Eggs	North America	Husband and Wohltmann 2011
	Podapolipus sp.	Locusts	Adult	Thailand	Usmani and Usmani 2018
	Astoma locustarum	Grasshoppers	Eggs and adult	North America	Walsh 1860
	Eutrombidium trigonum	Grasshoppers	Eggs, nymph, and adult	USA	Severin 1944
Reptiles	*Uromastyx hardwickii*	Locusts	Nymph	Rajasthan	Usmani and Usmani 2018
	Acanthodactylus cantoris	Locusts	Nymph	Rajasthan	Usmani and Usmani 2018
	Eremias argus	Grasshoppers	Nymph	China	Xunbing et al. 2016
	E. argus	Grasshoppers	Nymph	Mongolia	Huang et al. 2016
	Bufo bufo	Grasshoppers	Adult and nymph	United State of America	Dellonger and Day 2021
Birds	*Acridotheres tristis*	Locusts	Adult	India	Long 1981
	Pastor roseus	L&G	Nymph and adult	Russia	Belik and Mihalevich 1994
	Ciconia ciconia, Glareola nordmanni	Locusts	Adult	Africa	Lounsbury 1909
	Milvus migrans, Corvus alba, Falco naumanni, Circus pygargus	L&G	Nymph and adult	Niger	Falk et al. 2006, Petersen et al. 2008
	Chelictinia riocourii	Locusts	Nymph and adult	Africa	Pilard 2007, Mullié 2009
	Sturnus roseus	Grasshoppers	Nymph and adult	China	Ji et al. 2008
	Passer luteus	Locusts	Nymph	Mauritania	Kooyman et al. 2008
	Corvus splendens	Locusts	Adult	India	Usmani and Usmani 2018
	Egertta alba	Locusts	Adult	Africa	Sanyang 2001
Mammals	*Onychomys leucogaster, Spermophilus tridecemlineatus*	Grasshoppers	Adult	United State of America	Stevens 1989
	Procyon lotor	Grasshoppers	Nymph and adult	United State of America	Dellonger and Day 2021
	Vulpes velox	Grasshoppers	Nymph and adult	United State of America	Nevison and Day 2018
	Cynomys ludovicianus	Grasshoppers	Nymph and adult	United State of America	Russell and Detling 2003
	Homo sapiens	Locusts	Nymph and adult	Pakistan, Mexico, India	Samejo et al. 2021

(Hermann, 1804) (Acari: Microtrombidiidae). In its larval stage, it is parasitic on grasshoppers, and in its nymphal and adult stages, it is predaceous on the eggs of grasshoppers (Severin 1944, Sevsay and Karakurt 2013, Gupta and Kumar 2018). Previous studies suggest that mite larvae reduce grasshopper fecundity and mobility, making them useful for the integrated pest management of grasshopper populations (Anderson 2019).

Spiders.—Although the spiders (Araneae) are a diverse arachnid order consisting of more than 3,500 species in North America (Young and Edwards 1990, Duperre 2023), all are obligate predators, and many feed upon herbivorous pest insects (Dellonger and Day 2021). The orb-web weavers Araneidae and Tetragnathidae feed upon Homoptera, such as leafhoppers, Diptera, and Orthoptera, especially grasshoppers (Nyffeler et al. 1994, Moses et al. 2022). The spiders are probably the least studied of the L&G predators. Nine species of spiders have been reported as predators of grasshoppers, but the list is known to be incomplete and is undoubtedly much longer. The wolf spider, *Schizocosa minnesotensis* Gertsch, 1934), and a jumping spider, *Pellenes* sp., are two species of non-web builders that are often quite abundant on rangelands and are reported as predatory on various rangeland grasshopper species (Lavigne and Pfadt 1966, Mishra et al. 2021).

Birds.—Birds can reduce acridid densities by 30–50%. A survey of published accounts and other relevant sources conducted by Mullié (2009) revealed that at least 537 bird species from 61 families are currently known to prey on L&G in Africa. Several African bird families, such as Coraciidae and Laniidae, appear to be specialized acridivores (Yang and Gratton 2014, Kollross et al. 2023). A wide range of acridid species are recorded as food for Ciconiidae, Glareolidae, and Corvidae (Dellonger and Day 2021). Petersen et al. (2008) and Falk et al. (2006) found that the pre-migratory movements of Abdim's storks are in synchrony with the seasonal movements of Senegalese grasshoppers. Over 200 species of birds (e.g., grassland bird species) feed on grasshoppers (Wang et al. 1998, McEwen et al. 2000) and can aid in managing grasshopper populations. Sick and dying grasshoppers and locust hoppers, rendered sluggish by *Metarhizium*, have also been seen being taken by birds and frogs (Kooyman et al. 2003, Mullié 2021, Mullié et al. 2021). Many field experiments have shown that avian predation can substantially impact grasshopper populations (Branson 2005, Ji et al. 2008). In some areas of India and Pakistan, rose-colored starlings were claimed to have eliminated 50% or more of desert locust hopper bands. China is one of the few countries where bird predation, either natural or by herded ducks and chickens, is actively used as a very important contribution to biological locust control (Zhang and Hunter 2017, Shi et al. 2019).

Amphibians, reptiles, and mammals.—Locust remains found in droppings indicate that some mammals, such as foxes, skunks, opossums, raccoons, Japanese macaques, and geladas, also eat locusts (Price and Mitchell 2003, Kooyman et al. 2003). L&G are known for being important to the food web of various organisms, especially small mammals (e.g., ground squirrels, shrews, and mice) (Churchfield et al. 1991, Russell and Detling 2003, Dellonger and Day. 2021). Since small mammals reproduce quickly and require large quantities of prey to fuel a rapid metabolism, they can be an excellent resource for managing grasshopper and locust populations (Churchfield et al. 1991). Moreover, toads, frogs, lizards, and snakes also prey on L&G (Dellonger and Day. 2021).

Conclusion

Many varieties of natural enemies of L&G exist in nature, which underscores the complexity of the ecological relationships within these ecosystems. L&G cause substantial agricultural losses and environmental damage. Intricate networks of pathogens, parasites, and predators keep their populations below a certain level. At present, there are commercial formulations of entomopathogenic fungi, i.e., *Metarhizium acridum*, Green Guard® (Australia), Green Muscle® (UK, Africa), Novacrid® (Africa) and Metacridium® (Mexico). *Paranosema locustae* is formulated and commercially available in China. In this review, we explored the natural enemies of L&D, each playing a unique role in regulating their populations. Natural enemies are not only promising biocontrol agents but also help maintain ecological balance. By preserving their natural habitats and providing favorable conditions, we can foster ecologically sound and environmentally friendly management of L&G. Moreover, integrating these natural enemies with other sustainable pest control practices can reduce reliance on chemical pesticides to safeguard agricultural productivity and promote healthier ecosystems.

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