

What Have We Learned after Millennia of Locust Invasions?

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Abstract: Locust outbreaks have long been a very serious problem for agriculture and livelihoods in many countries globally. This article is an introduction to a Special Issue of the journal *Agronomy* devoted to the management of these pests. Although not exhaustive, the nineteen articles herein cover a variety of species, many regions of the world and many aspects of pest locust management and research in the early 21st century. This book is a source of information and reflection, as well as a resource, to support new areas of investigation and practice contributing to the process of developing sustainable solutions for locust invasions.

Keywords: locust plagues; control; management; preventive strategy; locust biology; locust ecology

1. Introduction

Since time immemorial, pest locusts in their gregarious phase have been a very serious problem for agriculture and livelihoods of human populations in many countries around the world. The economic and social consequences of locusts are so substantial that these highly migratory pests are treated as a national priority by many countries, and several international commissions have been established to unite efforts. The start of 2020 was marked by the continued South American Locust upsurge—the first major upsurge of this species in 60 years, as well as the onset of a dangerous Desert Locust invasion extending from Kenya to India—the first many of these countries have seen in decades. This Special Issue aims to shed light on the following overarching questions: What have we learned from historical outbreaks? What research is ongoing? What action is needed? How serious is the threat? How should the world respond to plagues today?

Around twenty-five of the estimated 6700 Acrididae (Order: Orthoptera) species [1] are considered to be major pest locusts to varying degrees [2–6]. When populations of these insects increase under favorable ecological conditions, they acquire gregarious and migratory behavior, leading to the formation of spectacular swarms that can migrate vast distances and leave behind devastated crops and desolation (Figure 1). However, these insects are also a source of food for various human populations [7], and swarms certainly have beneficial but largely unknown ecological roles [8].



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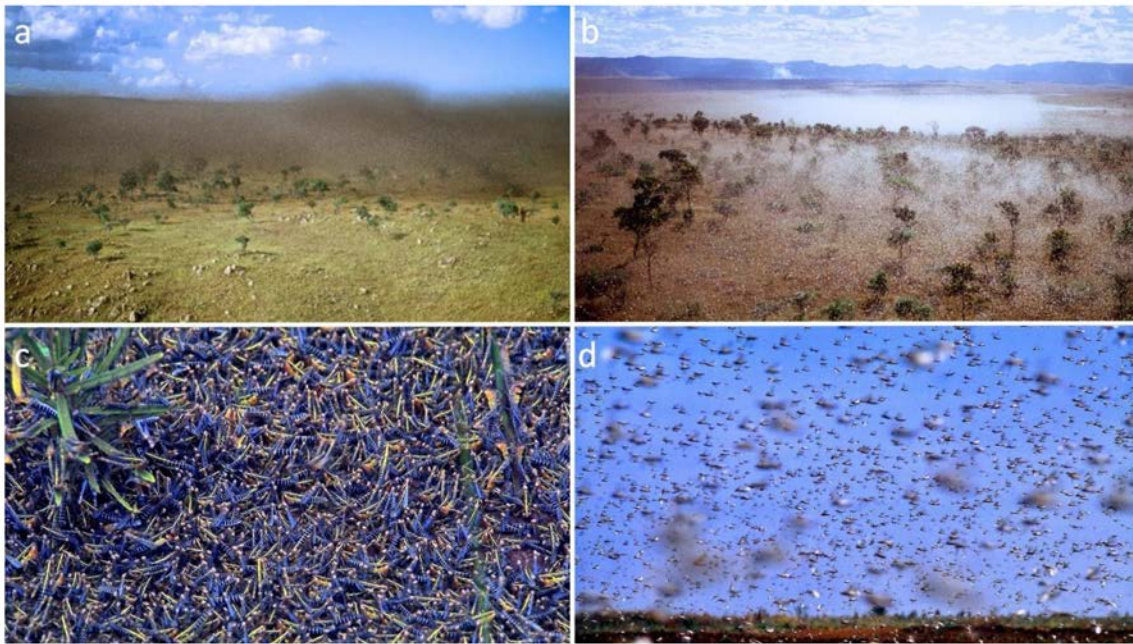


Figure 1. Example of locust swarms and hopper bands: the Migratory Locust, *Locusta migratoria*, in Madagascar (a,b) and the Mato Grosso Locust, *Rhammatocerus schistocercoides*, in Brazil (c,d) (photos M. Lecoq). The Migratory Locust swarm is approximately 5×2 km, measured from a helicopter, and it completely covers the landscape due to its high density. Its color varies according to the position of the observer in relation to the sun.

2. History of Locusts and People

Due to the extent of their devastation and the spectacular nature of their migratory swarms, locusts have left an indelible mark since ancient times in the minds, beliefs, literature and arts of many cultures all over the world [9,10]. The first mention of their damage—albeit conjectural—dates to Assyrian times, ca. 3200 BC, and was noted on a stone tablet in pre-cuneiform writing [11,12]. Since then, the evidence has multiplied, in numerous chronicles, books, religious texts, and testimonies of travelers, missionaries and naturalists throughout the ages [13–15]. Some cultures include attribution to locusts in the creation of the world and mastery of fire [16,17]. Locusts have also been used for political and military purposes [18–20].

Locust management has been ongoing for centuries, probably since the beginning of agriculture, as testified by ancient Egyptian, Chinese, Hebrew, Roman and Greek texts [9,21,22]. For example, China has 3000 years of recorded Migratory Locust outbreaks, with >800 outbreak episodes. The frequency of invasions led ancient emperors and their governments to impose treatment programs: full-time locust control officers were appointed in the Tang Dynasty in the eighth century [23]. Laws were also passed in the 11th, 12th and 15th centuries requiring local governors to conduct control, which included paying people to catch locusts and bury them in pits [23,24].

Over the centuries, more and more resources have been deployed on all continents. At the beginning of the 20th century, concerted international cooperation was developed (see, for example, [25–30]). Since then, research, surveillance and control efforts have steadily increased and been refined. In the present day, the Food and Agriculture Organization of the United Nations plays a centralized role in coordinating survey and control activities, strengthening national capacities and providing emergency assistance in response to locust upsurges and plagues [31–36].

3. 100 Years since Pivotal Phase Theory Published

This Special Issue coincides with the 100th anniversary of the phase theory Sir Boris Petrovitch Uvarov published in 1921 in a famous article [37–39]. The article demonstrated that locusts have two phases and that a single individual can shift phases in response to population density. The solitary phase is prevalent at a low density, avoids conspecifics, does not form swarms and is typically a cryptic green or tan color. The gregarious phase is prevalent when favorable ecological conditions support high-density populations; it then aggregates and migrates *en masse*, and typically has a combination of dark and bright markings. Prior to this discovery, the two phases were thought to be different species. This article corresponds to a pivotal, founding moment, from which the phenomenon of locust invasions began to be better understood. Phase theory became the major paradigm within which locust research has been able to flourish and develop effectively for a century.

After Uvarov's discovery, research was aimed at locating the so-called “outbreak areas”—areas of origin of the outbreaks, which were previously unknown—and studying the ecological conditions that supported the development of gregarious populations in these areas. Additional focal areas over the century included efficient and environmentally safer control methods, the real-time monitoring of field populations, and general biology and ecology, with a particular focus on the mechanisms of phase change. Several recent articles have masterfully reviewed these various topics [36,40–42].

The result of this research and scientific and technical progress is that outbreaks have now become less frequent and smaller in scale. If they do occur, they are now controlled quicker, although the damage caused can still jeopardize the food security of rural populations in many Global South countries [36]. Recent outbreaks of Desert Locust in Africa and Asia [43–45] and the South American Locust *Schistocerca gregaria* [46,47] are indeed reminders that the problem remains, albeit to a lesser extent than in the past. Each resurgence is a surprise to many—most often through unawareness—that this ancient and spectacular problem is still around. Beyond the immense scientific and technical progress attested by the reviews mentioned above, many lessons have been learned over the century.

4. A Few Key Lessons

(1) **The catastrophic impact of major locust outbreaks is a reality.** Despite denials and challenges in recent decades [48–50], the impact is real, devastating and documented, affecting not only crops but many aspects from family to national economics. Crop and pasture losses can lead to severe food shortages, large price fluctuations in markets, insufficient availability of grazing areas, the sale of animals at very low prices to meet household subsistence needs, high tensions between pastoralists and local farmers, and large human migrations to urban areas [36,51]. Impacts can reverberate for many years. Children born during plague years in impacted communities are less likely to ever start or to perform well in school [52,53]. Importantly, conventional techniques and simple cost–benefit ratios based on the market value of affected crops fail to capture true costs where >90% of crops are for subsistence. Furthermore, in the case of migratory pests such as locusts, the burden of control may fall on one region, while the benefits may be recorded completely elsewhere [54].

(2) **Prevention strategies have been shown to be effective where they have been applied** [55–57]. Advancements in locust biology since Uvarov's 1921 article revealed how plagues develop from pockets of gregarious locust outbreaks. These advancements created opportunities for preventative management involving the regular monitoring of high-risk areas and early treatment, in contrast to reactive control once a crisis has evolved. While prevention has been considered an unattainable goal [58], delayed control interventions lead to a locust situation that is overwhelming and exponentially more difficult and costly to manage [59]. Preventive management strategies for locusts have thus been developed with dedicated organizations set up in many regions globally; however, the sustainability of these management systems remains an important concern [55,60].

(3) **Current prevention strategies may not be widely feasible** since they require consistent resources and training and can be weakened by the erosion of infrastructure in the time between outbreaks, insecurity and war; however, community partnerships can help. If preventative management is successful, it inevitably leads to a vicious cycle with decreased investment when the problem is perceived to be solved [60,61]. Outbreaks then occur unfettered when ecological conditions become favorable. Regional insecurity and conflict can also preclude preventative management in key regions [62]. One aspect that has a clearer solution is the better engagement of communities in locust-prone regions. Prevention plans focused exclusively on the permanent surveillance of smaller outbreak areas that neglect surrounding rural communities during quiet periods and fail to inform them about the ins and outs of preventive control may prove to be largely counter-productive in the long term. Management plans that are better able to include local communities and learn from their traditional ecological knowledge through periods of calm as well as in the event of failure of prevention may be more apt to maintain their effectiveness over many years.

(4) **During major outbreaks, there continues to be pressures requiring the massive use of fast-acting insecticides.** The various shortcomings of preventative strategies continue to result in the development of large-scale outbreaks that directly threaten crops, thus requiring the massive use of fast-acting insecticides. This situation regularly raises controversy about the quantities used and their harmfulness. It habitually calls into question all preventive control strategies, forgetting—most often due to lack of information—their largely positive aspects. However, there are still no synthetic chemical pesticide alternatives that are viable on a large scale. Some biopesticides have been developed, most notably, the fungus *Metarhizium acridum*. Though, perhaps apart from China (Zhang and Hunter p.c. in [40]), many logistical challenges remain [36]. A targeted treatment option with limited secondary environmental impacts that takes into account the many inherent logistical challenges could make great strides in improving sustainable locust management.

(5) **Climate change is likely to alter the probability, severity and location of outbreaks** [63–65]. However, the level of understanding of the magnitude and directionality of impacts and responses of various locust species to climate change remains low [66]. In fact, in view of the many uncertainties, there is an urgent need to coordinate research and monitoring actions on the topic of global change [67].

(6) **With each new major outbreak, a similar cycle of events repeats itself.** As a locust crisis hits international headlines, consistent themes arise. The initial response is concern for the lack of action and food security, followed by the questioning of control strategies, profitability of control and environmental impacts. Emphasis on safer techniques leads to a multitude of miracle solutions being proposed (e.g., massive locust vacuums). Articles in the media flourish, many opportunistic scientific publications are born, and declarations of good intentions multiply, including developing new research in various fields, training people, reforming institutions and reinforcing their resources. Each major crisis has its share of recommendations, always more or less the same, but between two major outbreaks, the locust problem is quickly considered to be solved, the memory of the problem and of past outbreaks fades, vigilance is reduced and qualified personnel retire or are fired, resulting in a devastating loss of knowledge. In this way, major outbreaks succeed one another, regularly followed by collective amnesia. In this sense, locust plagues are no exception in the list of calamities that have affected humanity for millennia. This can be likened to the myth of Sisyphus, the hero of Greek mythology. Everything appears to be an eternal and absurd restart [68].

(7) **Transdisciplinary approaches are critical.** The situation of the repetitive cycle has long been denounced [60,61,69]. Despite the immense improvements in monitoring and control methods, if outbreaks remain—albeit at a more modest level than in the past—it indicates it is no longer only a problem of limited biological and technical advancements. It is also, and above all, a question of removing the obstacles linked to the way we, as a global community, approach the problem, and of realizing that we have always forgotten major components: people, human behavior, decision-making processes, and the hazards

of any human action. A better integration of social sciences in the process of developing sustainable solutions seems increasingly necessary, in addition to the more traditional approaches, which are obviously indispensable [61]. There is a need to develop a more comprehensive research, response, and resilience framework by engaging actors across disciplines, sectors, cultures, and boundaries. Supporting a global network to enable transdisciplinary approaches and continuity between outbreaks is part of the mission of the Global Locust Initiative at Arizona State University.

5. Summary of Articles Included in This Special Issue

This Special Issue covers a variety of species, many regions of the world, and many different aspects of locust management and research in the early 21st century. It discusses the Desert Locust—a major pest and model species—but also the Central American Locust, the Brown Locust in southern Africa, the South American Locust and the Italian Locust in the Siberian steppes. The aspects discussed are diverse: ecology and behavior; control strategies and methods; pesticides, their impact and substitutes; possible contributions from social sciences to improve the management of locust outbreaks, and even the positive aspects of locust invasions, both in terms of human nutrition and ecosystem health. Here, we present briefly the various contributions that constitute this Special Issue.

First, concerning the behavioral aspects, Maeno et al. [70] studied the previously poorly understood nocturnal behavior of swarms of the Desert Locust, *Schistocerca gregaria*. This nocturnal behavior appears to be predictable and dependent on plant size, and the authors propose that it can be used to facilitate locust swarm management and to adopt a general strategy of nocturnal locust control.

Using time series of abundance indices for the Desert Locust and the Oriental Migratory Locust (*Locusta migratoria*), Cheke et al. [71] analyzed them independently and in relation to measures of solar activity and ocean oscillation systems. The results suggest that solar activity can be used to predict locust abundance, offering hope that information on these phenomena might enable a better early forecasting of Desert Locust upsurges.

Liu et al. [72], for the first time, studied the behavior of Desert Locust swarms in southern Tibet at very high altitudes of up to 5400 m. They show that low temperatures, high humidity and low atmospheric oxygen put the locusts under severe stress and that the Himalayan mountains provided an important natural barrier that limited the northward expansion of Desert Locust populations.

Concerning management strategies, Showler et al. [59] discuss the three major approaches to Desert Locust population control: reaction, proaction and outbreak prevention. They suggest that while research on the biology and behavior of this species is no longer a highly urgent requirement for improving control efficacy, new research priorities have emerged for developing epidemic prevention capability (and for improving proactive management). Salient needs presently include long residual tactics for prophylactic (preventive) control in breeding areas; intervention thresholds; and improved, sustainable coordination among stakeholders at national, regional and international levels. The most recent Desert Locust episode of 2020 illustrates how prophylactic control could have prevented the entire upsurge, and how proactive management in some countries contained the spread of swarms.

Despite the high level of progress in recent years, Showler and Lecoq [62] show that locust surveillance and control are impaired by many obstacles, perhaps the most intractable of which is insecurity. After a historical analysis of insecurity in the various Desert Locust range countries, the 2020 upsurge is used to show how direct insecurity still contributes to the genesis and expansion of locust outbreaks. The possible mitigation of the effects of direct insecurity on some Desert Locust operations is discussed.

Sergeev [73] covers the eco-geographic distribution and long-term dynamics of the Italian Locust, *Calliptamus italicus*, in Asia, especially in Western Siberia, and analyzes their consequences for the management of pest species and rare forms. He discusses issues arising from insecticide experimental treatments, as well as ecological associations between

the Italian Locust and rare Orthoptera. Suggestions are provided regarding the need for the improved monitoring, supervision, control and forecasting of Italian Locust distribution and population dynamics.

Ciplak [74] provides a historical background for locust outbreaks in Southwest Asia (mainly Arabian Peninsula, Cyprus, Iraq, Israel, Jordan, Lebanon, Palestine, Syria and Turkey), assesses the potential for outbreaks of local species, and defines pathways for future actions, especially with regard to global change and agricultural expansion that may increase locust activities.

Barrientos et al. [75] present a review of the Central American Locust, *Schistocerca piceifrons piceifrons*, an important transboundary pest distributed from Mexico to Panama. The paper covers life history, habitat, ecology, permanent breeding areas, band and swarm formation, phase polyphenism, gregarization and migration. They provide a history of recent outbreaks and consider the current management strategy for this locust and recommended control measures, as well as current and future research.

In South Africa, the regular and often intense outbreaks of the Brown Locust, *Locustana pardalina*, are a formidable pest control problem. Price [76] discusses the operational constraints associated with the traditional ground control strategy in the Karoo outbreak area of this species. He makes recommendations for a modernized and technologically equipped integrated management strategy for the Brown Locust, combining ground and aerial tactics with the flexibility and capacity to effectively deal with outbreaks.

Trumper et al. [47] present a very interesting case of preventive management in the South American Locust, which has been successful for many years but has recently experienced a major resurgence. Their paper provides a review of this species' biology, management history and perspectives on navigating a plague period after a 60-year recession.

Monitoring and control methods have made many advances in recent decades, but challenges remain. Matthews [77] discusses the difficulties of regularly monitoring locust populations, often in remote and unpopulated areas, and the recent contribution of new technologies, particularly drones and mycopesticides. Drones would facilitate more efficient surveys, determining where sprays need to be applied at an early stage, and minimize the risk of swarms developing and migrating to feed on large crop areas. They could also spray groups of hoppers and adults. The use of biopesticides, which have been available for many years, is encouraged due to their effectiveness and greater acceptability to the environment and non-target fauna.

Control operations are naturally a crucial tool for managing locust crises. Retkute et al. [78] use the example of the recent Desert Locust upsurge in 2019–2021 to analyze the nature of control operations conducted to contain the crisis. These treatments were used both for the immediate protection of crops and to reduce overall locust numbers. Without the latter, the upsurge might have lasted many years as they did in the first half of the 1900s.

The harmful effects of pesticides used in locust control are illustrated by Peveling's article [79]. His studies in Madagascar show a long-term decline of harvester termites following multiple barrier treatments with fipronil carried out to control an outbreak of the Migratory Locust in the late 1990s. The main outcome of this research is a strikingly low resilience of harvester termite populations, which did not recover within eight years, with likely repercussions on food webs. The environmental benefit of barrier treatments is lost if the same areas are treated repeatedly during the same campaign. Recommendations are given as to how to mitigate those risks.

As we have seen above, biopesticides appear to be a promising and readily available solution to control locusts, though there are currently logistical barriers to their widespread use. Abdelatti and Hartbauer [80] propose an alternative treatment whose main component is linseed oil. The authors describe the impact of this formulation on the aggregation behavior of Desert Locusts. Their results suggest that linseed oil may act as a bioactive agent capable of disrupting swarm formation.

Protozoa may also be used to control locust and grasshopper populations. Zhang and Lecoq [81] reviewed the role of *Nosema locustae*, a biological agent developed in the 1980s for locust and grasshopper control. The authors review the many studies that have focused on pathogenicity, the host spectrum, mass production, epizootiology, applications, genomics and molecular biology. This entomopathogen has many benefits: lower environmental impacts, vertical transmission to offspring through eggs and long-term persistence in populations of locusts and grasshoppers for more than 10 years, and it is well adapted to a variety of ecosystems. However, some limitations still need to be overcome.

While locusts have been at the heart of the natural sciences for over a century, the social sciences remain vastly under-represented. The potential contributions of the social sciences to improve the management of locust plagues are explored by Therville et al. [61]. Organizational, economic and cultural variables clearly have a considerable impact on the management strategies of these pests, and the social sciences are an important means to better understand these questions. This article examines the scope and purpose of different subfields of the social sciences and explores how they can be applied to different issues facing entomologists and practitioners to implement sustainable locust research and management.

In a similar vein, Lockwood and Sardo [82] use the Desert Locust as an iconic case from a humanities perspective. They provide a summary of standard moral theories and examine their shortcomings in developing a framework for understanding the socio-economic complexity of locust management. They address some of the models of global justice and focus on two fundamental questions: Who is a moral agent in Desert Locust management? How can responsibilities be equitably distributed between agents in preventive and reactive modes? After identifying the agents, they use a quadruple set of principles to construct a Desert Locust management framework consistent with global justice and apply this conceptual system to two hypothetical scenarios.

While major locust outbreaks exacerbate food insecurity, locusts can also be a food source for many populations. Samejo et al. [83] conducted a field study in India to investigate whether locust collection could be an attractive control method to protect crops in the event of an invasion, as well as an accepted food resource for poor rural communities. The authors conclude that locust consumption could be an effective practice to prevent malnutrition and protein deficiency and, to some extent, a mitigating measure to help communities better protect themselves and their crops from locust invasions. They argue that the collection and consumption of locusts should be encouraged while being realistic about their actual impact on locust control. They also advocate that this should be carried out in concert with local authorities to minimize risks to human health by avoiding the consumption of insects treated with pesticides.

Finally, Kietzka et al. [8] further explore the ecological and human food value of locusts. They note that while locusts have been considered since the Antiquity to be very serious pests of sedentary agriculture in many parts of the world—and as such combated with increasingly sophisticated means—they can be a nutritious food source for people and of great ecological importance as major components of ecosystem nutrient cycling. The authors estimated their potential benefits for human nutrition and ecosystem function using calculations based on a 1 km² area of swarming and breeding Desert Locusts, *Schistocerca gregaria*.

Although not fully comprehensive, this Special Issue covers most major current issues in locust management. We hope that it will be a source of information and reflection for many already working in the field, as well as serving as a resource to support new areas of investigation and practice to aid in the process of developing sustainable solutions for locust outbreaks.

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