Global perspectives and transdisciplinary opportunities for locust and grasshopper pest management and research

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Abstract

Locusts and other migratory grasshoppers are transboundary pests. Monitoring and control, therefore, involve a complex system made up of social, ecological, and technological factors. Researchers and those involved in active management are calling for more integration between these siloed but often interrelated sectors. In this paper, we bring together 38 coauthors from six continents and 34 unique organizations, representing much of the social-ecological-technological system (SETS) related to grasshopper and locust management and research around the globe, to introduce current topics of interest and review recent advancements. Together, the paper explores the relationships, strengths, and weaknesses of the organizations responsible for the management of major locust-affected regions. The authors cover topics spanning humanities, social science, and the history of locust biological research and offer insights and approaches for the future of collaborative sustainable locust management. These perspectives will help support sustainable locust management, which still faces immense challenges such as fluctuations in funding, focus, isolated agendas, trust, communication, transparency, pesticide use, and environmental and human health standards. Arizona State University launched the Global Locust Initiative (GLI) in 2018 as a response to some of these challenges. The GLI welcomes individuals with interests in locusts and grasshoppers, transboundary pests, integrated pest management, landscape-level processes, food security, and/or cross-sectoral initiatives.

Keywords

Acrididae, basic and applied research, biocontrol agents, collective action, environmental governance, food security, Global Locust Initiative (GLI), livelihoods, *Locusta*, *Melanoplus*, *Metarhizium*, multidisciplinary research, *Oedaleus*, organizations, Orthoptera, *Paranosema*, *Schistocerca*, social-ecological-technological system (SETS), transboundary migratory pest

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Introduction

Locusts are grasshoppers (Orthoptera, Acrididae) that can form dense migrating groups as nymphal marching bands or adult flying swarms. Many locust species are adapted for living in drylands that have limited agricultural and human activity where they persist at relatively low population levels. However, when periodic population explosions lead to continent-traversing swarms, extensive consequences emerge as a complex social-ecological-technological system (SETS) (Ostrom 2007, McPhearson et al. 2022). Defining and understanding each component of the system and their linkages is critical for overcoming challenges in locust research, response, and resilience. Historic isolation between disciplines and organizations from different regions and sectors can create barriers to advancing a systems approach. To help overcome these barriers and initiate a dialogue, we brought together 38 coauthors from 6 continents and 34 unique organizations, spanning academic disciplines from the natural sciences to the social sciences, the arts, and humanities, as well as experts from local to international organizations involved in real-world locust and grasshopper management. Together, we provide an introduction and review of recent advancements of the main components that make up the SETS comprising the major management and research organizations (Fig. 1). We highlight key papers and questions while exploring historical connections and possibilities for expanding synergies.

Locusts exhibit an extreme form of density-dependent phenotypic plasticity known as locust phase polyphenism (Uvarov 1966, Pener 1983), which occurs in response to large increases in population density and affects a suite of morphological, physiological, and behavioral characteristics. Locusts exist on a continuum between two states. At one extreme, at low population densities, locusts exist in the "solitarious phase." Solitarious locusts actively avoid conspecifics and, like most non-locust grasshopper species, are commonly cryptic in appearance and behavior and generally less active. At the other extreme, locusts at high population densities exist in the "gregarious phase" in which they are attracted to conspecifics and form coherent groups that are adapted for migration as both marching juvenile bands and flying adult swarms. Depending on the species, gregarious nymphs may also exhibit conspicuous coloration. The capacity to be a locust has evolved independently multiple times, resulting in locust species with unique characteristics and many grasshoppers that exhibit locust-like qualities (Song 2011, Cullen et al. 2017). Locusts and grasshoppers are the central focus of myriad fundamental and applied research questions spanning from molecules to landscapes.

As a result of their swarming biology and voracious appetite for pastures and crop plants during outbreaks, these insects bring together diverse cultures and organizations. Swarms link stakeholders across large spatial scales where conditions in one location can affect the probability of locust outbreaks occurring in other regions. Intense outbreaks can trigger emergencies across multiple countries with very different socioeconomic, political, and ecological landscapes. For the desert locust *Schistocerca gregaria* (Forskål, 1775) (Lecoq and Zhang 2019), outbreaks often originate in remote and harsh locations and cross boundaries between states that are facing political instability, or potentially mutually distrusting or even actively hostile (Showler 2003, Showler and Lecoq 2021, Showler et al. 2021). The organizations involved in locust response and management range from local community groups to national governments and intergovernmental organizations and may include non-profits, research institutes and universities, and agricultural industries. These organizations vary politically and culturally and may manage locust and grasshopper species with distinct characteristics as well as other species of insect pests.

Swarms can also link stakeholders across long and variable time periods. In some countries, managing locusts and grasshoppers is an annual occurrence requiring treatment most years, which has been the case for the Central American locust *Schistocerca piceifrons* (Walker, 1870) (Lecoq and Zhang 2019) in Mexico and Central America. Alternatively, there can be up to 10 years between major outbreaks of the Australian plague locust *Chortoicetes terminifera* (Walker, 1870) (Lecoq and Zhang 2019) in Australia. Others, such as the desert and migratory locust *Locusta migratoria* (Linnaeus, 1758) (Lecoq and Zhang 2019) and the South American locust *Schistocerca cancellata* (Serville, 1838) (Lecoq and Zhang 2019), undergo recession periods that can last for many years or decades followed by rapid population growth resulting in swarms, migration, and extreme crop losses (Lecoq et al. 2011a, Latchininsky 2013, Medina et al. 2017).

Crises cause a cascade of reactions that may rely on preexisting networks or ones formed during an emergency. While the rapid assemblage of management campaigns under pressure to safeguard agriculture is often impressive, the infrastructure and progress made during major outbreaks are generally not sustained through the long periods of locust recessions. This leads to a vicious cycle (Lecoq 1991, Therville et al. 2021) in which an emerging outbreak, fueled by increased awareness in the international community and media, spurs the mobilization of resources and management campaigns with resulting gains in knowledge and infrastructure. However, as the outbreak dissipates and a recession of unknown length begins, motivation and support wane: infrastructure put in place during the crisis starts to break down, and the "oblivious phase" begins (Lecoq 1991, Therville et al. 2021). This period inevitably comes to an end when environmental conditions spark the beginning of a new outbreak, and the cycle repeats.

Many factors coincide to perpetuate this cycle. The cooperative links between management organizations, regional governments, donor countries, and non-profit/NGOs are often not strong enough or contextually relevant to be sustained during non-outbreak times. This is exacerbated by the extra challenge of working across cultures, disciplines, and organizations. Budgets run out or are diverted to other projects or crises. Donors become fatigued, and people with the necessary practical experience and expertise change jobs or retire, and institutional memory is lost. Finally, there may be simply a general complacency and lack of future planning. Sustained global efforts to build and maintain cooperative links throughout non-outbreak and outbreak years can help break this vicious cycle.

Improving locust research, response, and resilience begins by understanding the current state of the different disciplines and organizations involved as well as consideration of the opportunities to support transdisciplinary activities—activities that span professional boundaries between researchers and practitioners, including managers and agriculturists (Lang et al. 2012, Therville et al. 2021, Lecoq and Cease 2022a). There are powerful synergies to be had by applying the SETS framework to build robust networks to deal with future challenges. To encourage this progression, stakeholders from around the world gathered for the Global Locust Initiative (GLI) launch conference held at Arizona State University on April 12–14, 2018. This publication is based on those conversations and was expanded over the following years. At the conference, and in subsequent working groups, participants were

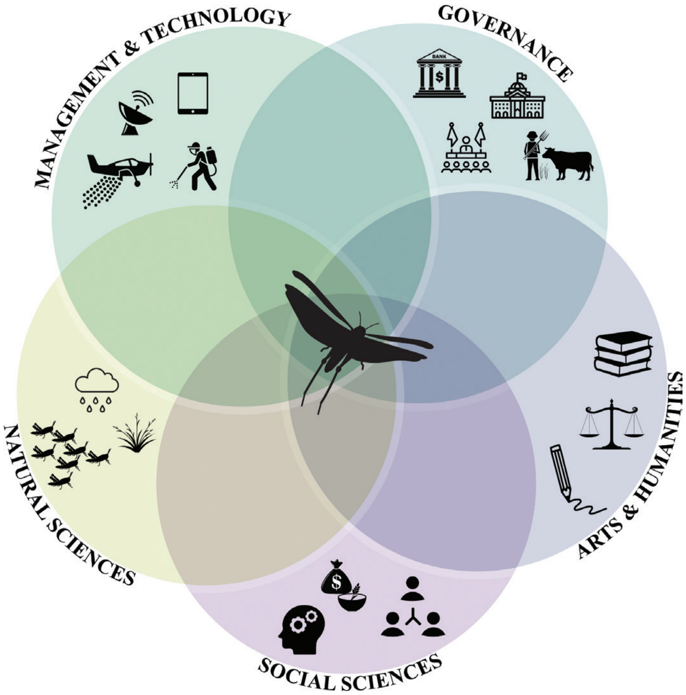

Fig. 1. A visual representation of the interconnected themes of the paper.

divided into discussion groups first based on regions of expertise (Asia, Latin America, Africa, Australia, and the United States and Canada) and then by discipline (management, natural sciences, social sciences, the humanities, and the ethics of locust control). Forty-four participants attended the conference, representing 28 organizations, 14 countries, and six continents (Suppl. material 1). Additional coauthors helped expand the disciplinary sections. This paper aims to serve as an overview of commonly discussed topics, a catalyst for transdisciplinary collaboration, and a guide to encourage growth of the field. Our main objectives are to 1) introduce the different disciplines and synthesize their recent advances and challenges, 2) explore the organizational networks involved in locust research and management in the attending countries, and 3) summarize challenges to sustainable locust management and propose visions for future development and collaboration.

Organizations and governance of locust control

Guiding discussion prompts

This section provides a comprehensive summary of the organizations involved in locust management but does not cover all the countries or organizations impacted more broadly by other members of the Acrididae family. We discuss the countries represented by conference attendees (Suppl. material 1). Participants were divided into focus groups by geographic region (Asia, Latin America, Africa region, Australia, and the United States and Canada). One additional group focused on the early history of research groups studying locust phase change, the interconnections among these groups, and how different organizations supported them over time. This brief history of locust research, necessarily partial, will serve here as an introduction to the current state of organization and governance.

In the region-specific breakout sessions, groups discussed how their organizations are connected through funding, sharing data/information, access to experts, training, or other mechanisms. These connections are complex and diverse. The organizations discussed ranged from village leadership to country and to the international level, including government and non-government organizations, banks, farmer organizations, universities, and intergovernmental agencies. The following sections present summaries and extensions of these conversations.

Brief history of phase change research

By Darron A. Cullen, Bert Foquet, Mira Word Ries, Stephen M. Rogers, Simon Springate, Michel Lecoq

A comprehensive overview of a topic as vast as locust phase polyphenism research from its inception was an impossibility. Thus, we focus mostly on Sir Boris Petrovitch Uvarov's key role and his major contribution to the internationalization of the problem of locust outbreaks. We did our best to expand on this using the various, mainly laboratory, work undertaken in the footsteps of Uvarov to show that, from the 1920s onwards, an increasingly large international community has been involved in this work. For the sake of brevity, we highlight only some of the most representative scientists and organizations. As we get closer to the present, the number of scientists and organizations involved grows more quickly, and it becomes difficult to be exhaustive. For most of the 19th century, much of the world was carved into the colonial empires of several European powers, particularly France and the United Kingdom. Locust research arose out of the scientific ideology and methodology developed through the social, political, and industrial revolutions of the 17th–18th centuries in Europe and the need to manage and exploit newly acquired imperial assets, which included the entire territories of most locust species. It is thus notable that modern locust phase research was largely led by two countries that were largely unaffected by locust outbreaks.

Early work on pest locusts began at the end of the 19th century, marked by the monumental work of a French pioneer in locust control and research, Jules Künckel d'Herculais, in the years 1888–1905 in North Africa on the desert locust, well before the discovery of the phase phenomenon (Kunckel d'Herculais 1905). In 1868, Charles Valentine Riley was appointed the first state entomologist of Missouri, the United States, where he studied the massive outbreaks of the Rocky Mountain locust, *Melanoplus spretus* (Walsh, 1866), wrote the book 'The Locust Plague in the United States' (1877), and prompted the establishment of the United States Entomological Commission. Among his suggestions for locust control were recipes for eating them. He later did foundational work on biological control and plant resistance involving other insect species.

However, Sir Boris Petrovitch Uvarov, born in 1886 in Uralsk, southeast Russia, was in many ways the father of acridology. At the age of 23, he became the director of the Entomological Bureau at Stavropol and got his first experience in the organized control of both the migratory locust *Locusta migratoria* and the Moroccan locust *Dociostaurus maroccanus* (Thunberg, 1815) (Lecoq and Zhang 2019). He observed mixed populations of the migratory locust and the apparently benign grasshopper *L. danica* alongside individuals with characteristics of both species. In 1913, his friend Plotnikov performed caged crowding experiments (Plotnikov, 1924), and Faure (1923) conducted field studies of the brown locust *Locustana pardalina* (Walker, 1870). These works prompted Uvarov to publish his theory of 'phase polymorphism' (Uvarov, 1921) (which later authors adjusted to the more scientifically precise 'phase polyphenism'; Pener 1991, Pener and Simpson 2009). Pivotal work demonstrated that the migratory locust and *L. danica* represent the two phases of the same species (*L. migratoria*) and that the change from one phase to the other is a function of population density, with the solitarious phase being prevalent at low densities and the gregarious phase prevalent when favorable ecological conditions support high-density populations. Uvarov then extended his theory to the desert locust *Schistocerca gregaria* and the red locust *Nomadacris septemfasciata* (Serville, 1838). While studying the specimens in the British Museum of Natural History, he realized from field records that the lone-living *Acridium flaviventre* (now considered a subspecies of the desert locust *S. g. flaviventris*) never co-occurred with *S. gregaria*. Relatedly, *A. coangustatum* (now a synonym of the red locust *N. septemfasciata)* never co-occurred with *N. septemfasciata*. He surmised that these were likely to be their respective solitarious forms (Uvarov, 1923). His phase theory was further supported by field observations of *S. gregaria* by King (1921) and Johnston (1926a,b) and of the closely related Central American locust *Schistocerca piceifrons* (then called *S. paranensis*) by Dampf (1926), who isolated wild-caught individuals and observed their transition toward a solitarious phenotype. Faure (1932) subsequently carried out caged experiments on *L. pardalina* with varying locust density, parentage, and humidity. Thus, the 1920s corresponded to a foundational 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 the past century (Lecoq and Cease 2022a).

In 1920, Uvarov relocated to London to join the Imperial Bureau of Entomology, later renamed the Imperial Institute of Entomology. In 1929, he became the head of the International Unit of Locust Research, initially composed of just him and his assistant Zena Waloff. In 1931, the Comité d'Etudes de la Biologie des Acridiens was created in France under the support of Professor Pasquier, based in Algeria. This committee was succeeded in 1943 by the Office National Antiacridien (ONAA), chaired by Zolotarevsky and assisted by Pasquier and Rungs, an office that ceased its activities with the independence of Algeria in 1962 (Roy 2001).

During the 1930s, in addition to Uvarov, many other scientists contributed to the nascent discipline of acridology. A major event of this period was the convening of several international conferences on the issue of locust outbreaks (Buj Buj 2016): Rome 1931, Paris 1932, London 1934, Cairo 1936 (which marked an important step for the internationalization of the problem), and Brussels 1938 (Ministère des Colonies 1938). These conferences brought together an increasing number of countries: the Union of South Africa, Saudi Arabia, Argentina, Australia, Belgium, Bulgaria, Canada, Chile, China, Egypt, Ethiopia, France, Greece, Guatemala, India, Iran, Iraq, Mexico, the Philippines, Portugal, Romania, Spain, Uruguay, the United Kingdom, the United States, and Yugoslavia, plus many representatives of other countries in Africa and Asia colonized by the British, French, Italian, and Portuguese. Among the many scientists who participated in these conferences (or played an important role in locust research during this decade) were D. Imms (UK), H.B. Johnston (UK), O.B. Lean (UK), R.C. Maxwell-Darling (UK), B.P. Uvarov (UK), H.J. Brédo (Belgium), P. Vayssière (France), R. Pasquier (France), L. Chopard (France), B.N. Zolotarevsky (France), J.C. Faure (South Africa), Y. Ramachandra Rao (India), and M. Afzal Husain (India, later Pakistan). The list of countries represented at the conferences demonstrates the broad global reach of the problem; the list of scientists, predominantly European and all male, demonstrates the narrow social and political base of locust research at this time.

The Anti-Locust Research Centre (ALRC) was established in 1945 in London, UK with Uvarov as director. The ALRC's primary aims were to coordinate research in acridology and secure international cooperation in locust control fueled primarily by the colonial economic interests of the British Empire. The same happened in the French Empire (Péloquin 2013, 2014). During this period, multiple field studies were undertaken on the main locust species of economic importance. Numerous advances were made in locust behavioral ecology, including a better understanding of life histories, migration, and its causes, as well as the interactions of locusts with their natural enemies. But the overriding focus of field work undertaken during this period was undoubtedly the identification of the areas where swarms ultimately originate from—variously referred to as gregarious, breeding, or recession areas. It was during this era that Zolotarevsky (1937) demonstrated that the accumulation of solitarious individuals in outbreak areas appeared to be the primary factor in phase transformation, which also depended on a set of ecological factors, such as climate and vegetation, that varied according to the species and regions concerned. By the end of the decade, outbreak areas were identified, at least roughly, for each of the most economically important locust species: *S. gregaria*, *L. migratoria*, *N. septemfasciata*, and *L. pardalina*. Additionally, the ALRC funded research on non-locust grasshoppers (e.g., Dirsh 1965).

Uvarov stressed the need for permanent programs to survey outbreak areas and develop international cooperation to contend with the strong migratory abilities of these insects. The dissolution of the European empires and the creation of many new independent countries, which accelerated following World War II, required a new approach to managing the locust problem. The formation of the Food and Agriculture Organization (FAO) of the United Nations in 1945 provided a cooperative international framework. Cooperation became a reality in the 1950s when the FAO helped to set up the Desert Locust Control Committee to promote international locust control cooperation. Since 1955, as mandated by its member states, the FAO ensures the coordination of desert locust monitoring and control activities and plays a major role in the early warning system via its Desert Locust Information Service (DLIS) (managed by the ALRC in London from 1943 to 1978, then by the FAO in Rome; see section titled "The humanities and ethics of locust control" below for more information on the role of the DLIS and other FAO commissions established around this time). International monitoring, control, and cooperation were gradually implemented, and international organizations were set up for permanent survey (FAO 1968, 1972, Hafraoui and McCulloch 1993, Roy 2001, Magor et al. 2005).

Throughout the post-war period of the 1950s and 1960s, and in the implementation of Uvarov's recommendations to develop interstate cooperation on locust problems, various other international organizations were created to deal more effectively with the various locust problems around the world. These organizations, mainly operational in nature to control invasions more effectively, have nevertheless played a key role in improving our understanding of the biology and ecology of locusts. We cannot be exhaustive, but the following are some of the emblematic organizations of this time:

- International Regional Organization of Plant and Animal Health (OIRSA) (est. 1947) for the Central American locust,
- International Red Locust Control Organization for Central and Southern Africa (IRLCO-CSA) (est. 1971 following the International Red Locust Control Service (IRLCS) 1949-70) for the red locust in Central and South Africa,

- Desert Locust Control Organization for Eastern Africa (DL-CO-EA) (est. 1962) for the desert locust in East Africa,
- Commission de lutte contre le criquet pèlerin en Afrique du Nord-Ouest (CLCPANO) (est. 1971) and Organisation commune de lutte antiacridienne et de lutte antiaviaire (OCLALAV) (est. 1958) for desert locust in North and Northwest Africa, both replaced by the FAO Commission for Controlling the Desert Locust in the Western Region (CLCPRO) in 2002,
- International African Migratory Locust Organisation (OICMA) (est. 1955), based in Mali and disbanded following financial difficulties in the 1980s and a greatly reduced importance of the Mali outbreak area as a result of modifications in its environment.

Although Uvarov retired in 1959, he continued working at the ALRC until his death in 1970. For a comprehensive obituary and history of the ALRC under his directorship, see Waloff and Popov (1990). Following his death, the ALRC's remit was broadened to include more general aspects of plant and animal protection in developing countries, and it became the Centre for Overseas Pest Research (COPR) in 1971. Many prominent locust phase-change researchers passed through the ALRC and COPR during or soon after Uvarov's stewardship. John Stodart Kennedy made field observations of encounters leading to aggregation and then gregarization in *S. gregaria* (Kennedy 1939); he later reviewed the extent to which phase change was responsible for swarms when compared to ecological factors (Kennedy 1956). Peggy Ellis pioneered arena-based behavioral assays, doing highly comparative side-by-side testing of *S. gregaria* and *L. migratoria* nymphs. These circular arenas test the temporal and spatial dynamics of phase-dependent aggregation (Ellis 1956, 1963a,b, Ellis and Pearce 1962), the onset and maintenance of marching after group formation (Ellis 1950, 1951, 1964a,b), and the effect of tactile stimulation on gregarization, which she achieved using small pieces of wire and crowding with woodlice (Ellis 1959). Behavioral work was continued by Sylvia Gillett (1968, 1972, 1973), including some of the earliest work on locust aggregation pheromones, which was investigated independently by Nolte and colleagues in South Africa (Nolte et al. 1973). Together with Graham Hoyle and David Carlisle at the ALRC, Ellis also explored the physiology of phase change (Ellis and Hoyle 1954, Ellis and Carlisle 1961). Hoyle later helped to establish locusts as a model organism in neurophysiology, continuing the proselytizing efforts of Uvarov to promote locusts as ideal experimental animals. Jeremy Roffey, George Basil Popov, and L.V Bennett explored the spatial and environmental processes that promoted the survival, multiplication, and gregarization of *S. gregaria*. Meir Paul Pener spent a postdoctoral year at the ALRC in 1964, going on to an eminent career investigating the physiology and endocrinology of locust phase polyphenism in Israel (reviewed in Pener 1991, Pener and Yerushalmi 1998, Pener and Simpson 2009).

Fieldwork in the 1950s and 1960s was a continuation of that undertaken in the 1920s and 1930s. For example, in Mali, within OICMA, important work was carried out on the process of gregarization in *L. migratoria* in the floodplain of the Niger River, specifying the movements and dynamics of its populations (Descamps 1953, Remaudière 1954, Davey 1959, Farrow 1975, among others). Additionally, various field studies were carried out on *N. septemfasciata* in its outbreak areas in Madagascar (Têtefort and Wintrebert 1967) and, within the IRLCO, in the African Great Lakes region, particularly in the Rukwa valley in Tanzania (Chapman 1959, Dean 1968, Morant 1947, Scheepers and Gunn 1958, Symmons 1963, Vesey-Fitzgerald 1964). Around the same period, from 1959 to 1964, the FAO played a particularly important role in locust research with a large project on *S. gregaria* directed by Belgian entomologist Hans Brédo, which was financed mainly by the United Nations Development Programme (UNDP) and included a major research component (FAO 1968). This project led to a significant advance in the ecology of the desert locust over its entire range, improving knowledge of the biotopes that favor gregarization (Popov 1965, 1997). The operational research part of this project was under the responsibility of Jean Roy, who was in charge of improving strategies and methods of intervention and control (Roy 2001).

A few years later in Madagascar, another UNDP-FAO research project was carried out from 1971 to 1973 to perfect a strategy for controlling the migratory locust. Directed by J.P. Têtefort, this project made it possible to better understand the functioning of the outbreak area of this species in the extreme southwest of the island. The project quantified the major influence of rainfall, highlighted the crucial role of the movement of solitarious populations in the gregarization process, and proposed a monitoring and warning system (Launois 1974, Lecoq 1975, 1995). Following this project, the Programme de recherche interdisciplinaire français sur les acridiens du Sahel, better known by its acronym Prifas, was created within the Groupement d'étude et de recherche pour le développement de l'agronomie tropicale (GERDAT), which later became The French Agricultural Research Centre for International Development (CIRAD). One of the first works was to carry out research on *O. senegalensis*, the Senegalese grasshopper, in West Africa following major outbreaks in 1974. This work allowed a better understanding of the cycle and dynamics of this species, which performs annual south–north migrations influenced by rainfall driven by the dynamics of the inter-tropical convergence zone. This research led to a first attempt to model this species as a monitoring tool (Maiga et al. 2008). Then, for more than two decades, in collaboration with monitoring and control agencies, Prifas worked in all tropical areas of the world on the ecology of locusts, population dynamics, and risk modeling to improve surveying and control strategies and methods. Among the main species studied were the desert locust, the migratory locust in Madagascar and Indonesia, the Mato Grosso locust, *Rhammatocerus schistocercoides* (Rehn, 1906), in Brazil, and the red locust in Madagascar. In 1998, Prifas was transformed into a research unit of CIRAD entitled "Locust Ecology and Control." In addition to its numerous research activities, the unit has been strongly involved in FAO's EMPRES program in West and North Africa for about 15 years. The CIRAD locust unit is now integrated into a joint research unit called the Centre de Biologie pour la Gestion des Populations (CBGP). CBGP has ongoing work, including locust genetics and risk modeling, that benefits from nearly 50 years of expertise and a large network of contacts in the field.

In 1983, COPR in the UK was amalgamated with the Tropical Products Institute to form the Tropical Development and Research Institute (TDRI), which then merged with the Land Resources Development Centre in 1988 to form the Overseas Development Natural Resources Institute (ODNRI). The ODNRI became the Natural Resources Institute (NRI) in 1990 and was transferred to the University of Greenwich in 1996. During this transition, *S. gregaria* stocks from COPR were used to start a colony in the Department of Zoology at Oxford, where they were initially used by Stephen J. Simpson and colleagues for comparative studies of feeding and nutrition alongside *L. migratoria* (Roessingh & Simpson, 1984) before becoming the focus of a renewed effort to study locust phase polyphenism. Following the earlier work by Ellis and Gillett, Roessingh et al. (1993) introduced a novel behavioral assay in which *S. gregaria* nymphs were tracked for 5–10 min relative to a group of conspecifics at one end of a rectangular arena. Unlike the group assays pioneered by Ellis, the Roessingh assay focused on one insect at a time with a greater focus on the organismal basis of behavioral gregarization.

The legacy of the history of locust research is that much of it is still conducted in and/or financed by the Global North. Many of the countries most severely affected by locust outbreaks have small endogenous research programs, and money is generally spent on demonstrably practical control measures rather than on research, which is viewed as being speculative. The Kenyan scientist Thomas Risley Odhiambo trained at the University of Cambridge, under entomologist and physiologist V.B Wigglesworth in the early 1960s, where he studied reproductive physiology in the desert locust. Among the 14 papers he wrote during this time was a letter to Nature (Odihambo 1965). Following a review of the current status of Science in Africa (Odihambo 1967), he had a vision of developing an African research center focused on African—and more broadly, pantropical—research with the aim of increasing agricultural production and combating tropical and vector-borne diseases. He strongly believed that science conducted in Africa should have improving the livelihoods of smallholder farmers at its heart. This led in 1970 to the creation of the International Centre of Insect Physiology and Ecology (ICIPE) in Nairobi, Kenya. Knowing that maintaining financial stability would be difficult at the start of the post-colonial world, he proposed that ICIPE be a focal center of excellence offering training and a research environment for African scientists from across Africa. From the 1990s onwards, important work has been carried out at ICIPE on locust behavior and ecology, especially the desert locust, their chemical ecology, and their biocontrol based on entomopathogens (Torto et al. 1994, 1996, Hassanali and Torto 1999, Hassanali et al. 2005).

The 1950s brought some of the first women recognized for their contributions to phase-change research, although gender progress has been slow. For example, a symposium held at the 2005 International Conference of the Orthopterists' Society, where "most of the major groups working on locust phase polyphenism were in attendance," consisted of only one in nine female speakers (Simpson et al. 2005). In 2016, a locust phase change symposium hosted at the International Congress of Entomology had three of nine female speakers. In 2018, the launch event for the Global Locust Initiative had 15 out of 49 female participants. Locust phase change research, like biology in general, with its endless complexity and far-reaching implications in its application, is greatly enhanced when stakeholder researchers represent a diversity of perspectives, including gender. It is thus encouraging to see a continuing focus on recruiting women and other underrepresented groups to graduate programs and research groups centered around locusts, including the NSF Behavioral Plasticity Research Institute and the Global Locust Initiative.

Current national, regional, and international organizations

Australia

By Chris Adriaansen, Ted Deveson, David Hunter, Douglas Lawton, Cathy Waters

Regional overview.—In Australia, locust and grasshopper pests are managed at multiple organizational levels, including federal and state agriculture departments, regional agricultural services, natural resource management agencies, and individual landholders (who may also be engaged through regional or national industry bodies). The structural arrangements differ in each state, reflecting the histories of the problem and consequent political responses. The amount of authority, autonomy, and engagement at each organizational level also differ significantly, a factor that can hinder or enhance the collective coordinated response to locust management.

While Australia has several pest locust species, the Australian plague locust *Chortoicetes terminifera* causes the most agricultural damage, especially in the southeastern states of New South Wales (NSW), South Australia, and Victoria. The recognition of this species as a national problem from the 1930s onwards resulted in periods of intense scientific research and varying levels of organizational and government involvement. Outbreaks of the migratory locust and the spur-throated locust *Austracris guttulosa* (Walker, 1870) are generally more restricted in their peak population levels and the geographical extent of their impact. Other grasshopper species also periodically arise as localized high-density pests, most commonly the wingless grasshopper *Phaulacridium vittatum* (Sjöstedt, 1920), yellow-winged locust *Gastrimargus musicus* (Fabricius, 1775), and the small plague grasshopper *Austroicetes cruciata* (Saussure, 1888) (see Table 1 for a full list of species).

Organizational relationships.—Australia has a strong network and advanced organizational capacity to monitor and manage locusts and grasshoppers. The connections between government agencies, universities, industry groups, and the private sector are well established. The Australian Plague Locust Commission (APLC) was established in 1974 in response to significant infestations of various locust species over many decades. The APLC is jointly funded by the Australian Commonwealth, New South Wales, Victorian, South Australian, and Queensland governments to monitor and manage populations of the three main locust pest species. Western Australia chose not to join the APLC and instead manage their own locusts, as locust outbreaks in that state occurred less frequently and were seen as being locally produced, although there is evidence of some exchange migration across the continent (Chapuis et al. 2011). Locusts' high migratory capacity means that pests from one state can easily invade another, and the APLC manages populations that pose a credible threat to agriculture in another member state. Treatments often occur before locusts reach cropping areas, which is an important part of an early intervention strategy. The four APLC member states contribute different levels of funding according to the long-term propensity for economic impact to their jurisdiction, with the Commonwealth providing matching funds.

The APLC gathers and disseminates information to all stakeholders. Locust occurrence information is gathered from vehicle-based ground surveys by APLC field officers, state and regional agency reports, and landholders. This information is combined with climatic and other data from third parties to formulate situation analyses and forecasts, which are provided in various formats across platforms. Planning and coordinating locust control activities occur primarily between the APLC and state agencies, who in turn coordinate the actions of regional agencies. State agencies also provide advice directly to landholders implementing their own control. In New South Wales, the state agency provides landholders with access to pesticides through the local land services divisions.

While the APLC maintains its own limited research and development capacity, much of the locust-related research has been undertaken by other parties. Prior to about 1990, most state agencies undertook locust-related research, while larger Australian universities had both entomology and agriculture departments, with locust research being a favored topic of both students and aca-

Table 1. The main distribution of economically important locust and grasshopper species in Australia.

Species	Common Name	Distribution
Austracris guttulosa (Walker, 1870)	Spur-throated locust	Savannah areas of the Central Highlands and northwest regions of Queensland, Northern Territory, and northern Western Australia
Austroicetes cruciata (Saussure, 1888)	Small plague grasshopper	Portions of southwestern and South Australia, New South Wales, Victoria
Chortoicetes terminifera (Walker, 1870)	Australian plague locust	Widespread on the mainland
Gastrimargus musicus (Fabricius, 1775)	Yellow-winged locust	Western Australia, Queensland, Northern Territory
Locusta migratoria (Linnaeus, 1758)	Migratory locust	Central Highlands of (and sometimes in southern) Queensland
Oedaleus australis (Saussure, 1888)	Eastern plague locust	Inland eastern Australia
Peakesia hospita (Bolívar, 1898) and other *Peakesia* species		Queensland, Western Australia
Phaulacridium vittatum (Sjöstedt, 1920)	Wingless grasshopper	Coastal areas of southern Australia
Urnisa guttulosa (Walker, 1870)		Inland areas of Western and South Australia, Northern Territory, western Queensland, and New South Wales
Valanga irregularis (Walker, 1870)	Giant grasshopper or hedge grasshopper	Australian tropics and subtropics

demics. With the subsequent decline of 'public good' research in Australia, the APLC had to refocus to integrate into broader topics for which funding is more available. For example, to gather the data needed for the APLC to demonstrate its environmental stewardship, locust-related research has become a small part of larger projects conducted by university ecology faculties. Consequently, the APLC investment in research collaborations has increased commensurate with the size of the total research project, while the scope of the locust-specific components has either remained stable or been reduced. Some research is still undertaken in-house by the APLC, but it is primarily focused on very specific topics, such as locust control pesticides and application technology.

Funding for APLC operations is provided by the five-member party governments, usually as a budget appropriation from their agriculture departments. In NSW, the funds are drawn from a pool of funds derived from a legislated levy on rural landholders. Consequently, regardless of where the APLC spends any of these funds, the spending must consider the benefits of all members. The APLC manages its internal budget for control, insecticide, surveys, and research, which allows for the carryover of unused funds in low locust population years as a buffer for years with major outbreaks. While the APLC does not provide grants to any other organization, it does collaboratively fund activities in research and development. Universities often use APLC funds as leverage to secure larger grants from national research funders.

Regional strengths.—Member parties often say that the development and maintenance of locust-specific expertise is the primary reason to continue funding APLC. As state and local agencies have experienced reductions in staffing and loss of specific expertise, the APLC must maintain a stable capacity to redress the regular changes that are now common in state agencies. Capacity for rapid response is facilitated through the carryover of annual unspent funds during years of reduced or low locust activities allowing sufficient funds to ensure early intervention in years of locust upsurge. The provision of training and expertise is not always limited to locust activity in Australia. The APLC continues to assist and advise in locust outbreak responses in other regions, particularly Africa and Asia. The APLC also provides non-technical operational assistance during other pest outbreaks within Australia, undertaking various functional roles.

A variety of other organizations have different levels of focus in responding to locust outbreaks. State agencies generally respond when several intrastate regions are affected to coordinate the responses of individual regional agencies. Some jurisdictions provide pesticides directly to landholders, facilitating individual property control. Agencies at all levels work to ensure that locust control addresses the potential impact on human health, the environment, and trade.

The differing thresholds for locust monitoring and control along the APLC state–regional–landholder continuum are complex. Several states do not commit resources to monitoring or control until an emergency is declared, while other states and the APLC undertake frequent monitoring of populations through field surveys and landholder contacts irrespective of population outbreaks. The focus of an individual landholder is farm-scale pest control for crop and pasture protection. At the other end of the spectrum, APLC control is for multi-jurisdictional population management and community benefit. This may result in landholders having to manage sizable local locust populations alone when a locust population falls below APLC's action threshold. However, the greater flexibility associated with landholder control can be used effectively to manage localized population pockets and provide localized early intervention to mitigate wider population build-up, thus highlighting the wider benefit of encouraging and facilitating control of small populations by individual landholders.

The focus on environmental and human health and safety is well established in Australia. The inclusion of a biopesticide (active ingredient *Metarhizium acridum)* as a control tool allows treatments near environmentally sensitive areas or for organic farms. However, more research is still needed to assess the potential adverse consequences of microbials on non-target Orthoptera seen in other countries (e.g., Argentina, Bardi et al. 2012). Environmental protection, biodiversity conservation, and waterbody management issues are the responsibility of natural resource management authorities such as the Rangeland Alliance and jurisdictional-based Natural Resource Management groups (NRM). The latter coordinates with landholders and local land services divisions in NSW to distribute pesticides and implement control measures while protecting the environment and human health through educational outreach programs.

Regional challenges.—A challenge for Australia is managing the risks of locust control, such as the failure of prevention efforts, over-use of pesticides, and environmental contamination, all of which can result in economic loss (Adriaansen et al. 2015). Australian agencies in partnership with the APLC focus on appropriate ways to address these risks and develop innovations for the future.

Expertise in locust management flows to and from universities, state agencies, and then on to landholders. However, the flow does not always go back up the chain, and improvements to the two-way flow are needed. Collaborations with universities are transient and focus on a specific project or grant, and there is a push for more transdisciplinary work between research universities and other agencies. Information transfer from state agencies to NRM groups is strong but can also be problematic due to interagency politics or diverging agendas. Much of the transfer of knowledge and information relies on personal relationships; transfer mechanisms need to become institutionalized if they are to continue.

Further challenges are likely to arise due to the potentially limited lifespan of the pesticides used by the APLC and others for locust control in Australia. As global agricultural chemical entities reduce the availability of older chemistry in favor of newly developed products, some of the products on which the APLC and others have spent decades refining dosage and application technologies to reduce off-target impact and maximize efficiency of use may no longer form part of the Australian approach to locust population intervention. Considerable development effort will be required to achieve equivalent outcomes with any new control agents.

Regional vision.—As rapid improvements to climatic, landscape, and other related information occur across the region, a core future objective will be to develop a more responsive and reliable system for forecasting locust populations in Australia. However, as recent seasons have clearly demonstrated, the likely increase in climatic variability across the region's locust habitat means that many more, and increasingly complex, factors will need to be accounted for if locust forecasts are to extend beyond just the next generation and truly become a sound planning tool upon which all actors can reasonably rely.

Core research into the response of locust populations to changing climate and habitat, including an understanding of why seemingly favorable conditions do not result in expected population explosions, is required. The results of these investigations will also need to be factored into the improved forecasting tools to be developed.

Skill and knowledge loss are also likely to become very apparent in the region over the coming decade. Many of the experienced researchers once aligned to now non-existent university entomology faculties have recently or soon will retire, while a similar scene will play out in various government agencies where locust management and response expertise has resided over the past 50 years. Effective succession planning for this is increasingly difficult in the absence of an emergent threat on which new recruits can hone the necessary skills.

Africa

By Michel Lecoq, Shoki Al-Dobai, Amadou Bocar Bal, Aliou Diongue, Mohammed Lazar, Marion Le Gall, Balanding Manneh, Mira Word Ries

Regional overview.—Many African countries are consistently and negatively impacted by locusts and grasshoppers (Table 2). The researchers present at the conference had expertise in the Sahelian region of Africa; thus, this will be our focus here. The Sahel is a unique, roughly 3 million km^2 biogeographic region situated to the south of the Sahara Desert. As defined by the United Nations, the Sahel is a political region composed of 10 African nations spanning from Senegal in the west to Eritrea in East Africa. In this region, the two most important locust species are the desert locust *Schistocerca gregaria* and the Senegalese grasshopper *Oedaleus senegalensis* (Krauss, 1877), a non-model locust (Lecoq and Zhang 2019). However, many other locust species, such as the Moroccan locust *Dociostaurus maroccanus*, as well as non-locust grasshopper pests often proliferate, causing significant crop damage throughout the continent (Lecoq and Zhang 2019).

The Desert Locust (Schistocerca gregaria).—The desert locust, distributed from Mauritania to India, is probably the most dangerous migratory agricultural pest worldwide. During plague years, they reproduce rapidly. The magnitude of their destruction is due to exceptional gregariousness, mobility, voracity, and swarm size, with hundreds of millions of individuals in a single swarm (Brader et al. 2006). A highly polyphagous species, the desert locust can expand its diet breadth, particularly in the gregarious phase (Despland 2005), and consumes natural vegetation and a wide range of food crops. They can swarm and destroy vast expanses of field crops, leaving fields completely defoliated and tree branches broken under their weight.

Desert locust outbreaks are treated as a national emergency because of the economic and social consequences of their invasions (Lecoq 2003). Some invasion cycles have lasted for more than 20 years, resulting in huge economic losses. Although invasions are better controlled today, they continue to cause significant damage to crops, threaten the long-term food security of local populations in the Sahel region, and greatly contribute to famines (Lecoq and Zhang 2019). Additionally, they aggravate poverty and increase the vulnerability of households that are already living in precarious conditions (De Vreyer et al. 2015). The Sahelian countries are home to several breeding zones where locust outbreaks can arise (including areas that are far from crop fields in the desert areas of Mauritania, north of Mali, Niger, and Chad), which require constant monitoring. For a preventive strategy to be successful, it must be continuously improved (Sword et al. 2010) because the costs of controlling an invasion that is not stopped early or properly monitored may total hundreds of millions of dollars.

The Senegalese Grasshopper (Oedaleus senegalensis).—The Senegalese grasshopper is the main acridid pest of food crops in the African Sahel. For over 20 years, controlling this species has been the main activity of the national plant protection services of the Sahel countries (Maiga et al. 2008). This species regularly causes damage to sorghum, maize, rice, and particularly millet—a key subsistence crop. Damage to millet seedlings, often by nymphs, can be severe, leading farmers to repeatedly sow crops until they run out of seeds (Kooyman and Lecoq 2019). The heaviest damage is usually inflicted on the ears of cereals in the milky-grain stage when the Senegalese grasshoppers return following the descent of the Inter-Tropical Convergence Zone (Le Gall et al. 2022). During high-density years, the number of grasshoppers can give the impression of a locust swarm. For in-depth information on the biology, behavior, and management of this species, see Le Gall et al. (2023).

Organizational relationships.—To understand the current organizational structure of locust and grasshopper control in the Sahelian countries of West Africa, review the brief history in "Locust and grasshopper preventative management and biopesticides."

In the 'front line countries' of North and West Africa (Algeria, Libya, Mali, Morocco, Mauritania, Niger, Chad), the national units for desert locust control play a key role in surveying outbreak-

Table 2. Distribution of most important locust and grasshopper species in Africa.

Species	Common Name	Distribution
Acanthacris ruficornis (Fabricius, 1787)*	Garden locust	Sub-Saharan Africa from the West African forest zone south to South Africa and east to Saudi Arabia and Yemen, Madagascar, and other Indian Ocean islands
Aiolopus simulatrix (Walker, 1870)*	Sudan plague locust	Sahelian zone, Horn of Africa, the Middle East, South Asia
Anacridium melanorhodon (Walker, 1870)*	Tree locust	Sahelian zone south of Sahara
Diabolocatantops axillaris (Thunberg, 1815)*	Devil grasshopper	Throughout savannah regions of tropical Africa from Cape Verde to Ethiopia, southern two-thirds of the Arabian Peninsula and Iran, south to Zimbabwe and Mozambique
Dociostaurus maroccanus (Thunberg, 1815)*	Moroccan locust	Countries around the Mediterranean in the west to Kazakhstan and Afghanistan in the east
Kraussaria angulifera (Krauss, 1877)*		The Sahel and Sudan zones from Senegal in the west to Eritrea in the east.
Locusta migratoria (Linnaeus, 1758)	Migratory locust	Widespread across the Old World, from sea-level to more than 4,000 m in Central Asian mountains.
Locustana pardalina (Walker, 1870)	Brown locust	Semi-arid Nama-Karoo regions of South Africa, southern Namibia, south-western Botswana
Nomadacris septemfasciata (Serville, 1838)	Red locust	Africa South of the equator, Madagascar, Mauritius, Réunion, Comoros Isolated populations in Lake Chad Basin, central Niger River delta in Mali, Cape Verde islands
Oedaleus senegalensis (Krauss, 1877)*	Senegalese grasshopper, Senegalese locust	Sahelian region of Africa from Cape Verde to Sudan, Middle East, India. In East Africa, species occurs south to Tanzania.
Schistocerca gregaria (Forskål, 1775)*	Desert locust	Africa north of the equator, skirting Mediterranean Europe, Middle East, Arabian and Indo-Pakistani Peninsulas
Zonocerus variegatus (Linnaeus, 1758)	Variegated grasshopper	Africa South of the Sahara, Ethiopia, Angola, DR Congo, and Kenya

* Species most important in West African Sahel and Maghreb (Lecoq and Zhang 2019)

prone zones, mainly in desertic areas far from cultivated zones. In the Sahelian countries, these units are autonomous and were created by the FAO EMPRES, which started operating in West Africa in 2006. To support these units, state members mandated the creation of the Commission for Controlling the Desert Locust in the Western Region (CLCPRO) to promote all actions, research, and training necessary to ensure effective prevention and control of desert locust invasions. CLCPRO and the national anti-locust units jointly cover the role previously held by the Organisation Commune de Lutte Antiacridienne et de Lutte Antiaviaire (OCLALAV), which was created in the 1960s but experienced financial difficulties and was ill-suited to the ecological and economic complementarities between the Maghreb and Sahel countries and their necessary cooperation to deal with desert locust.

The 1987–1988 desert locust outbreak shocked many regional and donor countries and triggered a renewal of organizational involvement and research on the desert locust (Lecoq 2001). Field experiments on grasshoppers and locusts were conducted in 1989–1990, in cooperation with the Malian Plant Protection Service and USAID, using biological agents, including *Paranosema locustae* and *Beauveria bassiana* (Johnson et al. 1992), with parallel comparative tests conducted with these isolates in North America (e.g., Johnson and Goettel 1993). At the time, the collaborative Lutte Biologique contre les Locustes et les Sauteriaux (LUBILOSA) project was launched and subsequently led to the development of a mycopesticide called the Green Muscle® (Lomer and Langewald 2001, Lomer et al. 2001), which is less frequently used (Magor 2007, FAO 2009), although there has been an uptake in usage in recent years (FAO 2021).

Although rainfall and the resulting food it produces are critical drivers for locust outbreaks, drought can also lead to gregarization by reducing vegetation availability and promoting locust aggregation, fueling swarming behavior and migration in search of food (Ellis and Ashall 1957, Despland et al. 2000). The great drought in the Sahel between 1973–1974 triggered widespread outbreaks of *O. senegalensis* and many other grasshopper species (Lecoq 1978a,b). The improvement in the desert locust situation at that time made it possible to address the long-standing problem of pest grasshoppers. Many projects, partnerships, and organizations were launched with the mission to improve response, prevention, organizational collaboration, and governance (Capinera 2008, Traore et al. 2014). Outbreaks of varying sizes continued regularly between countries and years. These grasshopper problems are now tackled by national plant protection organizations (NPPOs) and are frequently one of their major occupations. Similar to those of the desert locust, several outbreaks of the Moroccan locust emerged in the countries of North Africa, particularly during the 1970s and 80s. Between 2001 and 2015, Algeria also experienced high activity of this species causing enormous damage.

In the Sahel, the AGRHYMET Regional Center (ARC) provides the agrometeorological information essential for better monitoring of locusts and grasshoppers. The ARC was created out of the Permanent Inter-state Committee for Drought Control in the Sahel (CILSS) as a regional development system focused on agriculture and natural resource management. ARC collaborates globally with many research organizations, including the French Agricultural Research Centre for International Development (CIRAD), financial organizations, and NPPOs, often providing funding, disseminating information, training, research, oversight, and monitoring.

The ARC carried out two main projects on locusts and grasshoppers (Locust Control Support Project) from 2006 to 2009, funded by USAID West Africa Office, Crop Protection Directorate of CILSS member countries, and other partners. The PreLISS Project (Regional Programme for Environmentally Sound Grasshopper Control in the Sahel) from 2002 to 2010 was funded by the Danish International Development Agency (DANIDA), the National Environmental Research Institute of Denmark (NERI), and other partners.

Various international partners also provide technical or financial support to these national or regional organizations to improve surveys and locust and grasshopper prevention and control. For example, the World Food Programme (WFP) and its sister organization, the FAO, connect banks, donor funds, and brokering agreements and plans for aid to locust control efforts (insecticides, food assistance, cash transfer programs, etc.). France-based CIRAD also partners with CLCPRO, regional universities, and national anti-locust units and engages in collaborative research and information sharing. Most NPPOs also work with universities to share research and data, with transnational organizations for resources and funding, and with foreign governments who lend or donate pesticides, assist with conducting surveys, or provision control teams, aircrafts, vehicles, fuel, and other equipment.

Regional strengths.—West Africa has a long history of scientific and technical achievements in desert locust and Senegalese grasshopper control. These advancements are enhanced by international cooperation with organizations like the FAO EMPRES program and the recent creation of autonomous national anti-locust units dedicated to desert locust control with their own budget (a strong step forward even if weaknesses exist in various countries). Regional and national locust contingency plans have been established, and estimates of the economic and social impact of the desert locust have increased the value of the preventive control strategies. New financing systems add strength with diverse and complementary sources adapted to the needs of each phase of desert locust population dynamics (Deshormes 2011).

The West Africa region has made substantial progress in anchoring the locust preventive control strategy principles, learning from the 2003–2005 desert locust upsurge and its consequences. CLCPRO plays a vital role in keeping all member countries actively engaged in the implementation of preventive control strategies. To maintain the preparedness of member countries for emergencies, CLCPRO provides capacity-building, institutional, and financial support.

Regional challenges.—International and national donors must be convinced to provide greater and faster support both for crises *and* long-term acridid management. When there is an alert, lengthy administrative delays in releasing funds and the funders' slow responsiveness must be avoided. Skills and mobilization of survey teams must be maintained over long recession periods, particularly as the periods of calm extend as control becomes more effective. Emergency planning is challenging, as technical and legal systems differ between countries. Some redundancy between organizational missions and mandates causes impediments or competition in receiving significant or consistent funding. Political insecurity in desert locust front-line countries such as Mali, Niger, and Chad creates further challenges (Showler and Lecoq 2021). Furthermore, while the desert locust captures much of the attention and funding, an efficient sustainable management strategy has yet to be developed for *O. senegalensis* and other grasshoppers, although new long-term approaches are emerging.

Regional vision.—Within the next five years, this region would greatly benefit from more sustainable pest control methods—improved biological control agents, such as mycopesticides, and integrated pest management—in addition to chemical pesticides (with proper application and disposal). The Sahel region needs a defined, effective, sustainable control strategy and increased research on *O. senegalensis* and other pest grasshoppers that enhances evidence of the species' impact on food security in the Sahel. Improved coordination and collaboration within the various organizations and the private sector will avoid redundancy and imbalances. We would also like to see increased funding by national governments for grasshopper research and management, including training for preventive management with sustainable solutions and the development of risk management and resilience capacities.

The FAO and CLCPRO will continue supporting member countries to strengthen their capacity and enable national locust control centers to operate with the autonomy and resources needed for regular survey activities and early response to outbreaks. For example, CLCPRO is expanding its membership beyond the current 10 countries (Algeria, Burkina Faso, Chad, Libya, Mali, Mauritania, Morocco, Niger, Senegal, and Tunisia) by adding three new countries (Gambia, Cabo Verde, and Cameroon). This will enhance cooperation in the region, boost the mandate of CLCPRO, and expand the benefit of technical support and technologies offered by the commission to the new countries for better regionwide implementation of preventive locust control strategies.

An important component of the future vision is to develop remote monitoring tools to better digitize population dynamics, particularly in localities with political insecurity. A new prediction model is under development by CLCPRO and CIRAD that will allow better adaptation, facilitate preventive control in the face of climate change, and add value to the monitoring and early warning system. In 2021, CLCPRO acquired 16 customized drones to enhance the locust survey capacity of its member countries. The FAO and CLCPRO are currently (2023) testing new locust survey drone prototypes and developing a customized locust control drone prototype that will be ready for field testing in 2023–2024. Introducing drone technology for locust survey and control is extremely valuable in areas where access by ground teams or aerial operations is difficult and/or dangerous.

Lastly, pesticide risk reduction remains one of the most important priorities for the FAO and CLCPRO. Implementation of Environment, Health, and Safety Standards (EHSS) is a core pillar of the locust control campaign. The EHSS have been widely adopted in the Sahel, and further promotion of these standards should remain a priority. With few desirable options for chemical pesticides, joint efforts by the FAO, research institutions, and the private sector are needed to start a dialogue and develop cooperating programs that can bring new, safer products to the market in the near future and replace hazardous and phased-out chemical pesticides. On the road to eliminating chemical pesticides, it is possible to reduce their use in combination with phenylacetonitrile (PAN) (Bal and Sidati 2013). A stock of *Metarhizium*-based biopesticides has been put in place by FAO/CLCPRO for the preventative control of the desert locust throughout Sahelian countries, but so far, only the National Center for the Desert Locust Control of Mauritania has used it to treat small areas.

Asia

By Alexandre Latchininsky, Mira Word Ries, Long Zhang

Regional overview.—Locusts and grasshoppers are a major threat to food security in Central Asia, Southeast and Southwest Asia, and China where there are several economically important locust species (Table 3). The most important is the migratory locust, *Locusta migratoria,* which is mainly distributed in China (the annual infested area in China is more than 5 million ha (Zhu et al. 2013)), Central Asia (primarily Kazakhstan and Uzbekistan), and Japan. In outbreak years, the densities of migratory locust hoppers can be very high at more than 1000 individuals/m^2 (Zhu et al. 2013). The

Table 3. The main distribution of economically important locust and grasshopper species in Asia.

Species	Common Name	Distribution
Calliptamus italicus (Linnaeus, 1758)	意大利蝗, Italian locust	China, Kazakhstan, Kyrgyzstan, Russia, Tajikistan, Uzbekistan,
Ceracris kiangsu (Tsai, 1929)	黄脊竹蝗, Yellow-spined bamboo locust	China, Laos, Myanmar, Thailand, Vietnam
Dociostaurus maroccanus (Thunberg, 1815)	摩洛哥蝗, Moroccan locust	Afghanistan, Iran, Kazakhstan, Kyrgyzstan, Russia, Tajikistan, Turkmenistan, Uzbekistan
Locusta migratoria (Linnaeus, 1758)	飞蝗, Migratory locust	China, Indonesia, Japan, Kazakhstan, Malaysia, Mongolia, Myanmar, the Philippines, Russia, Uzbekistan
Oedaleus decorus asiaticus (Germar, 1825) The taxa *Oedaleus asiaticus* Bey-Bienko, 1941 is now considered a junior synonym of *Oedaleus decorus* (Germar, 1825)*	黑条小车蝗, Mongolian locust	China, Mongolia, Russia, Kazakhstan
Schistocerca gregaria (Forskål, 1775)	沙漠蝗, Desert locust	Afghanistan, India, Iran, Oman, Pakistan, Saudi Arabia

*Cigliano MM, Braun H, Eades DC, Otte D. Orthoptera Species File. Version 5.0/5.0. [10 April, 2023]. http://Orthoptera.SpeciesFile.org.

desert locust, *Schistocerca gregaria*, is found in Iran, Yemen, Oman, Saudi Arabia, India, and Pakistan. From 2019 to 2021, these countries suffered a very serious desert locust infestation. The yellow-spined bamboo locust *Ceracris kiangsu* Tsai, 1929 has been a serious problem in Vietnam and Lao PDR since 2014. This locust forms large swarms in Northern Lao PDR and Vietnam, infesting five and eight provinces, respectively, with reported damages of approximately 60–90% of rice yields in Lao PDR (Spurgin 2016). Another serious threat is the Moroccan locust, *Dociostaurus maroccanus,* which is distributed in the dry foothills of Afghanistan, Iran, South Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan where it can infest over one million hectares. Infestations of the Italian locust, *Calliptamus italicus* (Linnaeus, 1758), are located in dry steppes all over Central Asia but primarily in Kazakhstan. During outbreaks, this species can infest approximately 10 million hectares.

Organizational relationships.—Organizations involved in locust management include transnational organizations (FAO), federal agencies, and research universities or institutes. China has developed an integrated national protocol to address locust outbreaks involving multiple institutions at all levels of the government. Although challenges still exist, coordination between different agencies results in an efficient response to control and mitigate the impact of locust outbreaks (Li et al. 2023). In China, some of the important research organizations are the Chinese Academy of Sciences (CAS), China Agricultural University (CAU), the Chinese Academy of Agricultural Sciences (CAAS) at the national level, and some provincial institutes. The CAS, CAU, and CAAS have been conducting locust studies for 60 years funded by China's national natural science foundation, the Ministry of Agriculture and Rural Affairs, the Ministry of Science and Technology, and some other institutes. Biological control, locust biology, ecology, locust physiology, and molecular biology are priority research areas. China also promotes basic research on locusts in molecular biology, locust olfaction, and pathology.

In Japan, the study of locusts is a priority of the Japan International Research Center for Agricultural Sciences institutes, particularly in terms of the biology of locusts and the mechanisms of phase change. In Kazakhstan, the Kazakh Research Institute for Plant Protection and Quarantine in Almaty has a long history of studying locusts and developing monitoring and control techniques, including the use of remote sensing, drones, and biopesticides. Similarly, the Uzbek Institute for Quarantine and Plant Protection has extensive experience in locust biological control. Some of the above organizations have established very effective and long-term collaborations in locust biology and control research. The School of Zoology at Tel Aviv University has a group studying locusts since 1999. In Iran and Pakistan, there are agricultural universities with some locust expertise, such as the University of Tehran College of Agriculture & Natural Resources, and the Department of Zoology at the University of Sindh, Jamshoro, Sindh-Pakistan and the University of Agriculture Faisalabad.

In this region, countries are subject to the locusts' capacity to migrate across shared borders. The transboundary species include migratory, desert, Moroccan, Italian, and yellow-spined bamboo locust. However, few collaborative strategies have been developed for controlling locusts near borders. China and Kazakhstan established a collaborative agreement for locust control near their borders that has been maintained for 17 years. Furthermore, all Central Asian countries (Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan) and Afghanistan participate in the Programme to Improve National and Regional Locust Management in Caucasus and Central Asia (CCA), implemented by the FAO since 2011 thanks to joint funding from the Japan International Cooperation Agency, Turkey (under the FAO-Turkey Partnership Programme, United States Agency for International Development (USAID)/Office of U.S. Foreign Disaster Assistance, as well as FAO resources (Technical Cooperation Programme (TCP) and Regular Programme). Its overall objective is to reduce the occurrence and intensity of locust outbreaks in the CCA, safeguard the food security and livelihoods of rural populations, and minimize the impact of chemical control operations on human health and the environment.

The Programme has created a regional technical network to address the three main locust pests (Italian, migratory, and Moroccan), strengthen national capacities in locust management, and bring greater attention to human health and environmental protection. Innovative geospatial tools, such as the Automated System of Data Collection and the Caucasus and Central Asia Locust Management System called CCALM, have been introduced. Both tools facilitate the regular sharing of locust information between countries. The FAO has issued regional monthly bilingual (English and Russian) bulletins during locust campaigns since 2010 and maintains the Locust Watch in CCA website.

The FAO contributes to locust control efforts through the TCP and the Regional Plant Protection Organization (RPPO). The TCP provides technical expertise to member countries through specific short-term projects, while the RPPO helps oversee and organize NPPOs who work directly on plant quarantine, pesticide use, and pest management technique implementation. The FAO Commission for Controlling the Desert Locust in South-West Asia (SWAC), established in 1964, is the oldest and smallest of the three FAO regional desert locust commissions with only four member countries (Afghanistan, India, and the Islamic Republics of Iran and Pakistan). SWAC sessions are held every two years, with host locations rotating between member countries. SWAC activities help to strengthen the national capacities of its member countries in terms of desert locust surveys, control operations, reporting, training, preparedness, contingency planning, emergency response, bio-pesticides, and human health and safety. SWAC emphasizes the importance of intra- and inter-regional collaboration and cooperation when implementing desert locust early warning and preventive control to minimize the duration, frequency, and intensity of desert locust plagues.

Productive border country cooperation is exemplified by Iran and Pakistan. Every April since 1995, the two countries have conducted a month-long joint survey of the spring breeding areas on either side of their common border in southwestern Pakistan and southeastern Iran. The results are used to plan the summer campaign. Since 2005, the Locust Directors and Information Officers (DLIOs) from India and Pakistan have attended a 'Joint Border Meeting' held on the border each month from June to November to exchange information about ongoing survey and control operations. Each year, the DLIOs from the three frontline countries (India, Iran, and Pakistan) attend a regional and interregional workshop with the FAO Commission for Controlling the Desert Locust in the Central Region (CRC) for updated training on data management and analysis. Regional workshops and cross-border surveys take place annually among Central Asian countries in the framework of the above-mentioned FAO Programme.

Regional strengths.—Within Asia, there are strong management programs in place for locusts. China has built a successful locust management program that includes regular surveys, forecasting, and control actions often using biopesticides (Zhang and Hunter 2017). Stakeholders at various administrative levels, including national, provincial, municipal, and county, are involved without duplication in locust management and response processes (Li et al. 2023). This forms the basis for an effective integrated pest management program that treats 50,000 to 100,000 ha of locust/grasshopper infestations with the biopesticides *M. acridum* or *P. locustae* each year, although chemical pesticides are still used (see Li et al. 2023 for more information). When outbreaks occurred in other countries in Asia, China has often been able to help (Phithalsoun and Zhang 2018), with the result that cooperation in locust management is becoming the consensus. For example, there are collaborative mechanisms for the management of the yellow-spined bamboo locust between China and Lao PDR, Vietnam, and Myanmar and for the management of the migratory locust between China and Kazakhstan. For the past decade, countries in Central Asia have benefitted from the FAO Locust Watch program in CCA, which has increased regional cooperation and knowledge sharing. CRC, SWAC, and the Programme (for CCA locusts) ensure coordination of efforts and cooperation between countries as well as the promotion of innovative tools and technologies for monitoring and control. Overall, most countries in the region rely on their own funding for locust management, making them less dependent on donor funding. Two countries—Tajikistan and Uzbekistan—have established specialized national locust control organizations responsible for survey and management.

Regional challenges.—The variable nature of locust management programs was demonstrated by the 2019–2021 upsurge in the desert locust. While some countries (e.g., Saudi Arabia and Iran) had a rapid response to the upsurge soon after it began in early 2019, other countries (Pakistan and India) had a slower response due to an initial lack of funding and resources, but the treatment programs were very successful once resources were put in place in 2020. However, regional conflicts in some areas severely limited control, representing one of the significant challenges to an effective desert locust control program. The lack of consistent funding for research and development inhibits implementation of the latest technologies in reaction to the situations in each country. The transboundary nature of *L. migratoria*, *S. gregaria*, and *C. kiangsu* requires an increasing level of regional cooperation, but such cooperation can be extremely difficult when there is regional instability (Gay et al. 2017, 2021). Political conflicts between certain countries create obstacles for locust monitoring and management, especially in border areas. For example, the situation in Afghanistan in 2022 precluded any international involvement or assistance under the aegis of the United Nations.

Even where there is relative security, there may still be much variation in the ability of countries to effectively manage locusts due to a lack of resources during recession periods, lack of knowledge of the latest technologies, and, most importantly, a lack of consistent funding, which leaves some countries relying heavily on donor funding during locust outbreaks. Some countries, such as Lao PDR and Pakistan, are on a tight budget for locust management due to low state revenues and a lack of entomologists, particularly locust management specialists. These shortages translate to longer response times by local or international funding, allowing outbreaking locust populations to increase to much higher levels before effective management is put in place. Thus, the region needs to continue to strengthen its collaborative monitoring and forecasting efforts as well as extend control campaigns to neighboring countries when highly migratory locust species outbreak.

Regional vision.—In the near future, we expect to establish several stronger collaborations for locust control, such as between Western Asian countries and the FAO, Western Asian countries and China, Southern Asian countries and the FAO, Southern Asian countries and China, and Western Asian countries and Russia. Sustainable and preventive locust management is important to the region's future. Two technologies were recently highlighted: biological control, mainly using microbials such as *M. acridum* and *P. locustae* (see section "Brief history of phase change research"), and information technology, used to increase the efficiency of monitoring, forecasting, and control action. China is a strong leader in both regards, focusing heavily on biological and preventive management strategies and maintaining a widespread network of field stations (Zhang and Hunter 2017). It is likely that the percentage of biological control in other countries will increase quickly due to China's leadership. However, there is still limited funding, relatively low amounts of research, and a paucity of high-level researchers. In addition, the most serious threats to locust control are the politically insecure areas in Western Asia, Afghanistan, and the India–Pakistan border.

Another important issue is the possible creation of the FAO Commission on locusts in CCA. As of December 2022, several countries in the region have given their support for the idea, and the issue is being considered by FAO higher administration. Such an organization would be less dependent on external funding and contribute to the sustainability of regional locust management.

Latin America

By Maria Marta Cigliano, Juan Pablo Karnatz, Carlos E. Lange, Mario A. Poot-Pech, Eduardo Trumper

Regional overview.—In Latin America, acridid outbreaks are a recurrent problem causing significant economic damage to agriculture: the Central American locust, *Schistocerca piceifrons*, and the South American locust, *Schistocerca cancellata*, have had recent upsurges (Medina et al. 2017, Poot-Pech 2017). Population densities of the Central American locust are high almost every year, with a recent increase in México, El Salvador, and Nicaragua. The South American locust had recurrent outbreaks, the last one occurring in 1954, especially in northwestern Argentina. Extensive campaigns to control hopper bands seem to have prevented the development of large plagues for over half a century (De Wysiecki and Lange 2005, Pocco et al. 2019) but in July 2015, the worst plague in more than half a century began in Argentina, with upsurges initiating in Bolivia and Paraguay in 2017 (Medina et al. 2017) and continuing at least until early 2021.

Two other locust species that periodically cause economic damage in Latin America are the Peruvian locust, *Schistocerca interrita* Scudder, 1899, and *Schistocerca piceifrons peruviana* Lynch Arribalzaga, 1903 (Morales 2005, Duranton et al. 2006). Outbreaks of the Mato Grosso locust, *Rhammatocerus schistocercoides*, occur in the *cerrado* (savannah) area of Central Brazil and in the *llanos* (grassland plains) of Colombia and Venezuela, where it is a significant pest (Lecoq and Pierozzi 1995). Grasshopper pests in the region are *Tropidacris cristata dux* (Drury, 1773) in Central America and *Tropidacris collaris* (Stoll, 1813) in South America. Recently, *T. cristata dux* has significantly damaged crops; it is also considered very responsive to climate change (Poot-Pech 2019). During the last two decades, *T. collaris* has consistently increased its population density, with damage to crops and trees in specific spots in north-central Argentina. *Bufonacris claraziana* (Saussure, 1884) often reaches pest levels in the large steppes of Argentine Patagonia, causing serious damage to forage and rangeland. *Dichroplus maculipennis* (Blanchard, 1851), a major pest species in the Pampas and Patagonia of Argentina and also considered a non-model locust (Mariottini et al. 2015), and *Dichroplus elongatus* Giglio-Tos, 1894, widely distributed in Chile, Uruguay, Southern Brazil, and Argentina, are regarded as two of the main grasshopper pests in Argentina, particularly in the Pampas and the fertile valleys of northwestern Patagonia (Cigliano et al. 2014, Carbonell et al. 2022) (see Table 4 for the full list of species).

Organizational relationships.—In each Latin American country, the National Service of Agriculture/Food Health and Quality oversees, executes, and assists in the control and management of locust and grasshoppers. In most cases, these activities are coordinated by regional phytosanitary protection organizations, such as International Regional Organization of Plant and Animal Health (OIRSA) in Central America and Comité de Sanidad Vegetal del Cono Sur (COSAVE) in South America. In 2019, by recommendation of the International Plant Protection Convention, the Inter-American Coordinating Group in Plant Protection (GICSV) was created with experts from the different regional organizations to evaluate the status of various pests, including locust species.

Research on Acrididae is mostly conducted by national and state/provincial organizations and universities that promote science, technology, and agriculture. The *S. cancellata* problem in Argentina is managed by interconnected stakeholders, including public and private organizations. The planning goes through a hierarchy from national to provincial and municipal organizations (Fig. 2). The National Food Safety and Quality Service (SENASA), through its Locusts & Grasshoppers National Programs (L&GNP), plays the central role of coordinating and implementing monitoring and control campaigns and maintains a permanent monitoring program in breeding areas (Fig. 2). The National Ministry of Agriculture, Livestock and Fisheries charges SENASA with

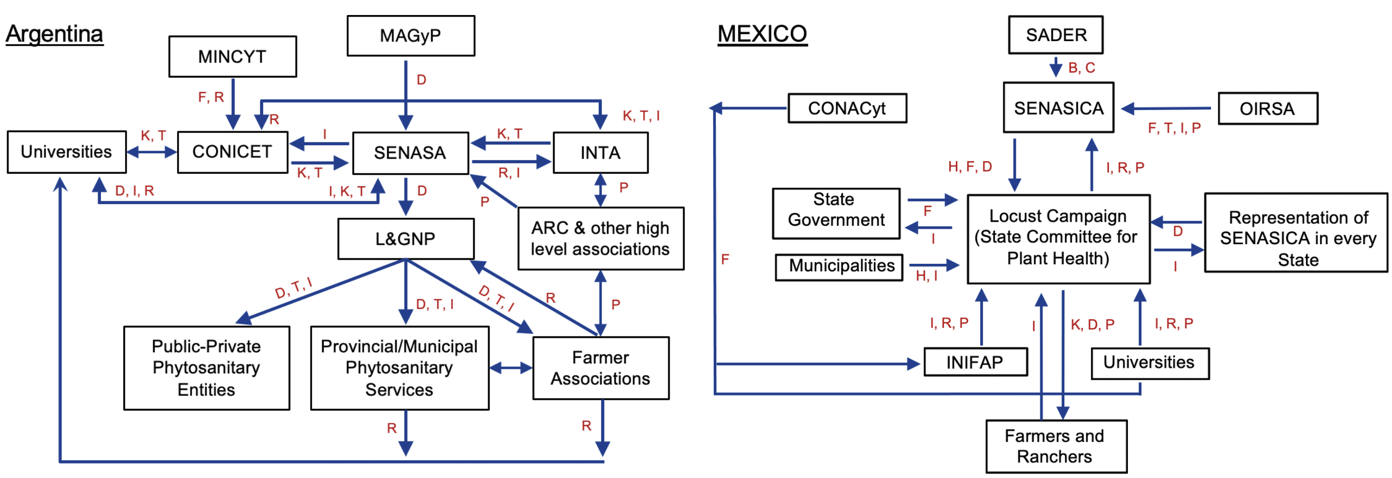

Fig. 2. Schematic representation of the main stakeholders and their relationships, directly or indirectly involved in locust governance in Argentina (left) and Mexico (right). Arrows represent the flow of directives/resources/requests. Letters represent different types of interactions. D: Directives, regulations; F: Financial resources; H: Human resources; I: Information; K: Knowledge; P: Proposals; R: Requests (knowledge, technology, information, and training; T: Training. **Argentina figure legend:** MINAGRO (National Ministry of Agriculture, Livestock and Fisheries), MINCyT (National Ministry of Science & Technology), SENASA (National Service of Agriculture/Food Health and Quality), CONICET (National Council of Scientific & Technological Research), L&GNP (Locusts & Grasshoppers National Program), INTA (National Institute for Agricultural Research), ARC (Argentinean Rural Confederations). **Mexico figure legend:** SADER (The Secretariat of Agriculture and Rural Development), SENASICA (The Service for the National Health for Food Safety and Food Quality), CONACyT (National Council for Science and Technology) OIRSA (International Regional Organization for Agricultural Health), INIFAP (National Institute of Agricultural and Livestock Forestry Research).

Table 4. The main distribution of economically important locust and grasshopper species in Latin America.

Species	Common Name	Distribution
Bufonacris claraziana (Saussure, 1884)	Toad grasshopper	Argentine Patagonia
Dichroplus elongatus (Giglio-Tos, 1894)	Elongated grasshopper	Chile, Uruguay, Southern Brazil, and Argentina (Pampas and northwestern Patagonia)
Dichroplus maculipennis (Blanchard, 1851)	Spotted-wing grasshopper	Pampas and Argentine Patagonia
Rhammatocerus schistocercoides (Rehn, 1906)	Mato Grosso locust	"Cerrado" area of Central Brazil and in the "llanos" of Colombia and Venezuela
Schistocerca cancellata (Serville, 1838)	South American locust	Northwestern regions in Argentina Bolivia, Paraguay, Uruguay, Chile, Southern Brazil
Schistocerca interrita (Scudder, 1899)	Peruvian locust	Peru
Schistocerca piceifrons peruviana (Lynch Arribalzaga, 1903)	Peruvian locust	Peru and Ecuador
Schistocerca piceifrons piceifrons (Walker, 1870)	Central American locust	Mexico and Central América, except in Panamá
Tropidacris collaris (Stoll, 1813)	Blue-winged or quebrachera grasshopper	Most of South America, east of the Andes and north of approximately 38 degrees south
Tropidacris cristata dux (Drury, 1773)	Giant grasshopper	Mexico and Central America

controlling locusts, and SENASA allots an operational budget to the L&GNP. During outbreaks, implementation is done by provincial and municipal levels of public administration, to national and provincial, and down to the sub-provincial level of private stakeholders. During an outbreak, L&GNP asks agronomy schools to participate in crisis committees where instructions and regulations, training, and information are delivered. Economic resources do not flow directly from SENASA to farmers but sometimes through straightforward control operations. The primary responsibility for pest control on private land lies with the individual landowners or tenants, with provincial and municipal administrations providing support personnel and/or critical supplies, such as pesticides and fuel, or contract aerial application services. Whether to involve academic, science, or public technology organizations to develop management solutions is determined both by independent initiatives from the scientific community and by circumstantial requests by SENASA and/or the National Agricultural Technology Institute (INTA).

In Mexico, the Secretaría de Agricultura y Desarrollo Rural (SADER) allots resources for the agricultural sector, which are later delegated to the Servicio Nacional de Sanidad, Inocuidad y Calidad Agroalimentaria (SENASICA), to attend to plant health projects and the annual budget for the locust campaign. Some state governments contribute to the campaign. SENASICA, federal government representatives, and the state government monitor and develop the locust program objectives and administrate expenditures.

If there is a demand for locust research, Consejo Nacional de Ciencia y Tecnología (CONACYT) calls for grants to fund proposals submitted by the state university, Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), or SENASICA. OIRSA coordinates between countries for outbreak control, training, diffusion, and support with a budget for emergency management.

Regional strengths.—Technical coordination occurs at different levels: continental (GICSV), regional (OIRSA, COSAVE, Andean Community (CAN), and North American Plant Protection Organization (NAPPO)), and national. When these organizations meet, they analyze and propose measures for prevention and management during a plague. The recent locust plague in Argentina, Bolivia, and Paraguay strengthened the interactions among the national organizations in Argentina and raised opportunities to interact with international organizations such as the Inter-American Institute for Cooperation on Agriculture (IICA), GLI, and CIRAD.

The recent *S. cancellata* outbreaks provided the opportunity to evaluate the management strategies, review knowledge of the ecology and biology of the South American locust to improve control measures, and outline research needs. In 2020, the first online course on locusts (preventive approach) for Latin America (organized by OIRSA) was held, as well as the first continent-wide meeting for the management of Orthoptera plagues in Mexico, to review plague status, conduct training, and exchange experiences.

SENASA, INTA, National Scientific and Technical Research Council (CONICET), and National University of La Plata (UNLP) (the last two through CEPAVE and Museo de La Plata) are currently collaborating in Argentina on research spanning the biology, ecology, and population dynamics of *S. cancellata* (Pocco et al. 2019, Trumper et al. 2022). Historically, however, research on systematics, biology, ecology, and biocontrol of pest grasshoppers in Argentina has mostly been carried out at CEPAVE and at the Museo de La Plata.

Regional challenges.—Stakeholder and regional cooperation are required for the successful, resource-efficient management of locusts and grasshoppers. If information flow is restricted, countries or regions lose the opportunity to share expertise, experiences, perspectives, tools, and infrastructure. Although efforts have been made to include a variety of organizations around the planning table, there is still much room for improvement.

One challenge is to build a comprehensive roadmap on which each action (research, development, innovation) and the role of each stakeholder is clearly identified. For example, Argentina lacks a strategic planning framework and should establish a hierarchy of objectives at different time scales and identify available expertise and infrastructure. A theory of change (Oberlack et al. 2019) should include a plan to blend action protocols across regions. A unified set of criteria expressed in one shared protocol would strengthen coordination across countries. Such a protocol could help guide the switch from reaction to prevention.

Most efforts to develop forecasting models lean on the availability of large databases that include as many variables as possible to capture the robust empirical relationships between insect density/presence and environmental factors. This can be obtained by collecting data from the whole range of geographical and historical sites. Unfortunately, very rarely do monitoring databases in Latin America fulfill this requirement. In the case of *S. cancellata*, efforts to systematize and centralize these data have only recently begun.

General research funding is insufficient for the following topics: biology, behavior, and ecology of locust/grasshopper pests; biological alternatives in acridid management; the effects of climate change, including potential increased variability in locust populations; development of forecasting models for early warning, monitoring innovations (remote sensing) and control (drones); identification of environmental variables that affect reproduction and gregarization thresholds of *S. cancellata* to be used in forecasting maps.

Organizational social capital and technician training are not preserved in regions where locusts and grasshoppers have very long periods of recession. Increasing training to strengthen disaster prevention and risk reduction is required. Long periods of recession threaten to erode the social capital of well-coordinated efforts among stakeholders. Robust governance networks of complex common-pool environmental problems are difficult to achieve and require time and resources. Individual staff and organizations should not have to reinvent the wheel each time a new outbreak occurs.

Like other regions, Latin America has a high dependence on synthetic pesticides, which have a high risk to environmental and human health (especially for applicator technicians). This necessitates further efforts to incorporate biological control (microbial agents) in some regions and increase its use in others.

Regional vision.—We envision a strategic framework for diligent, sustainable, environmentally friendly acridid management based on a robust cooperation network within Latin America and supported through strong links with experts and organizations in the international community. The management strategy should focus mainly on prevention built on smart, scientifically sound decision-making support systems (information, knowledge, analysis, and forecasting tools) as well as the development of contingency plans for a range of upsurge-invasive plague stages and scenarios.

The United States and Canada

By Derek A. Woller, Mira Word Ries, and Dan Johnson

Regional overview.—The Rocky Mountain locust, *Melanoplus spretus* (Walsh, 1866), once swarmed the Great Plains of North America from Canada to Colorado and was the most significant agricultural pest prior to 1900, with the largest recorded swarms of any locust worldwide (Lockwood and Debrey 1990, Lockwood 2004). Indeed, the origins of the U.S. Department of Agriculture's (USDA) focus on insect pests can be traced to this locust (Henneberry 2008). Amazingly, what appear to be the last specimens were found in Canada in 1902, and the species was formally declared extinct in 2014 by the International Union for Conservation of Nature (IUCN) (Hochkirch 2014). However, cyclical grasshopper outbreaks of other pest species still plague farmers and ranchers, especially in the rangeland habitats of the western United States and the prairie provinces of Canada, where annual surveys have been conducted since 1920 (Belovsky et al. 1996–2000, Johnson 1989b).

Out of more than 400 grasshopper species in the western United States and Canadian prairies, only about two dozen grasshopper species across three acridid subfamilies (Gomphocerinae, Melanoplinae, and Oedipodinae) can cause economically impactful crop damage annually due to population outbreaks (Dysart 1996–2000, Pfadt 2002, Johnson 2008). Of these, *Melanoplus sanguinipes* (Fabricius, 1798) is the most damaging pest species in the USA and in some southern areas of Canadian grassland (Pfadt, 2002, Johnson 2008) (see Table 5 for a list of six economically important species in the United States and/or Canada). In regions north of 53 degrees, *M. sanguinipes* has represented less than 1% of the grasshopper community in recent years, with the major grasshopper pest species in western Canada being *M. bivittatus* (Say, 1825), *M. bruneri* Scudder, 1897, and *Camnula pellucida* (Scudder, 1862) (Johnson 2022, unpublished data based on 12,000 identified survey specimens over four years). Grasshopper outbreaks were particularly devastating in the 1930s and mid-1980s, and, in fact, it was the outbreaks of the 1930s that gave rise to the USDA program that is currently mandated by Congress to manage such outbreaks, known as the Animal and Plant Health Inspection Service (APHIS) Rangeland Grasshopper and Mormon Cricket Suppression Program (Cunningham, 1996–2000). This program, working alongside the USDA's Agricultural Research Service (ARS), is continually improving management methods, working closely with several university research groups as well as a variety of federal (e.g., the Bureau of Land Management [BLM]), state (e.g., departments of agriculture), tribal (e.g., councils), and private stakeholders (e.g., ranchers with acreage for experiments). Additionally, to combat the many extant locust plagues outside of the United States, USAID offers support mainly via funding at the local level but also for visiting expert researchers.

Organizational relationships.—Information is the major connection between North American locust management organizations. The knowledge reservoir includes research, data, and researchers as well as their associated programs. Like Australia, North America is shifting toward more transdisciplinary and collaborative organizational relationships focused more on innovation and rangeland health than just responding to emergencies.

In the United States, best practices for grasshopper management are often publicly disseminated in bulletins, handouts, websites, and other publications (usually at the federal and state levels) because the goal of all stakeholders is the same: to safeguard agricultural interests from economically devastating outbreaks. Historically, local management efforts were prone to failure since the threat is mobile (Cunningham, 1996–2000), which is why the United States decided to tackle the problem at the federal level and bring together partners from many backgrounds (Cunningham 1996–2000, Henneberry 2008). Often, funding flows from the federal government to cooperators working on different research avenues. For example, the largest collaborative U.S. project to date was initiated in 1987 by USDA-APHIS: the Grasshopper Integrated Pest Management (IPM) Project, which resulted in a wealth of knowledge that was shared in a public document: the Grasshopper Integrated Pest Management User Handbook (1996–2000). Relationships established during this project, many with universities, are still active, in addition to new ones that are continually developed to pursue the same overarching goal. U.S. locust management knowledge has been shared internationally as part of collaborative projects with Canada (e.g., a project focused on population forecasting), Mexico (e.g., a project focused on modeling the potential migration of the Central American locust, *Schistocerca piceifrons*), and more distant countries, such as Australia, whose APLC invited members of APHIS to visit in the 1990s as part of a reciprocal information exchange.

Canada's prairie provinces—Manitoba, Saskatchewan, and Alberta— house many of the organizations involved in locust and grasshopper research and management. In Canada, grasshopper surveys during the early 20th century were the duty of the De-

Table 5. Six economically important grasshopper species in the United States and/or Canada (in alpha order by genus and then specific epithet) (Pfadt 2002, Johnson 2008, Cigliano et al. 2023).

Species	Common Name	Distribution
Aulocara elliotti (Thomas, 1870)	Bigheaded grasshopper	Western North America
Camnula pellucida (Scudder, 1862)	Clear-winged grasshopper	Western North America, northeastern United States, and southeastern Canada
Melanoplus bivittatus (Say, 1825)	Two-striped grasshopper	North America (widespread)
Melanoplus bruneri Scudder, 1897	Bruner's spur-throat grasshopper	North America (widespread)
Melanoplus packardii (Scudder, 1878)	Packard's grasshopper	Western North America
Melanoplus sanguinipes (Fabricius, 1798)	Migratory grasshopper	North America (widespread)

partment of Agriculture (now called Agriculture and Agri-Food Canada) in cooperation with counties and municipalities. Federal research stations supervised the surveys and made maps of the breeding populations in late summer using pins and colored pens, up to the first application of PC-based GIS for insect pest forecasting (Johnson and Worobec 1988). Currently, the surveys are the work of provincial agriculture departments in cooperation with counties and municipalities, which employ surveyors to record grasshopper densities and collect specimens for species determinations. Biological data, monitoring, and forecasting are made available by Manitoba Agriculture, Saskatchewan Agriculture, and Alberta Agriculture and Irrigation. The Prairie Pest Monitoring Network, which includes federal and provincial experts, industry representatives, and university researchers, makes maps and holds meetings to discuss grasshoppers and other agricultural pests. In British Columbia, industry and levels of government collaborate when grasshoppers become a problem in interior rangelands and crops.

Strengths and challenges.—The regional structure of grasshopper management in the United States has many strengths. Highlights include the availability of high-quality datasets for sociodemographic variables that make it possible to study the impacts of locust outbreaks and pest control, retention of historical knowledge in numerous publications, and the federal government's commitment to using a congressional budget line to permanently fund management research, annual population surveys, and treatments. Another highlight is the ability to unite stakeholders from diverse backgrounds across the country to investigate management methods that are improved, less expensive, and more sustainable. Such partnerships have led to innovations in technology and chemistry that suppress populations better before and during outbreaks. Examples of these include the use of the insect growth regulator insecticide diflubenzuron, which inhibits proper molting during non-adult instar stages (Foster and Reuter 1996–2000), and the use of the reduced agent and area treatments (RAATs) method, which typically involves alternating insecticide treatments with skipped, untreated areas of habitat, thereby lowering the amount of insecticide applied and its impact on the environment and non-target organisms, as well as reducing the overall cost (Lockwood et al. 2000).

Weaknesses in the regional structure of the United States include a decline in researchers who focus on grasshoppers and their IPM. The number of grasshopper specialists seems to wane in correlation with the perception of grasshoppers as a threat, which has declined due to less frequent outbreaks, possibly as a result of improved management methods. Despite this perception, high-density grasshopper populations are still common, and outbreaks occur periodically (often annually), as many ranchers and farmers will attest. Unfortunately, funding (federal and beyond) has dwindled, also potentially because of perception. This funding decrease is then directly correlated with a decrease in available personnel for annual federal surveys of population levels and treatments and may even be correlated with the decline in grasshopper researchers. Finally, another weakness is the inability to easily share data archives between federal and non-federal researchers due to the possibility of sharing private information about stakeholders related to outbreaks.

Regional vision.—We envision increasing public participation, education, and outreach to study and maintain rangeland habitat health. Such efforts will contribute to developing the sustainable management of grasshoppers by further publicizing the steps being undertaken and bringing in partners with new ideas. We advocate for adopting and developing new technology for increased ecological sustainability by investing in biocontrol, unmanned aircraft systems (UAS), molecular technology, forecasting, and other novel management methods and enhancing survey and monitoring efforts. Transdisciplinary research is the cornerstone of all these ideas and should continue.

The United Nations

By Chris Adriaansen, Alexandre Latchininsky, Michel Lecoq, Mira Word Ries, Clara Therville

Intergovernmental organizations often work on global scales, coordinating efforts in multiple countries, activating emergency responses, or sustaining efforts in long-term development initiatives. The FAO, the World Food Programme (WFP), and the United States Agency for International Development (USAID) are examples of these global actors. With locust outbreaks, world organizations supply meta-population management logistics, providing resources (monetary or expertise) and transmitting knowledge and resources to a broad range of actors. Understanding who these actors are and how they interact can serve to strengthen relationships, identify more grounded research questions, reinforce systems of communication for early warnings and reports, and avoid redundancy of services.

FAO: A global actor in desert locust control

Responsibility for desert locust forecasting and control coordination passed from the UK to the FAO in the 1950s. Today, the FAO has a mandate to monitor and manage the most dangerous locust pest, the desert locust. Based on the recommendation of the working party on desert locust control, the FAO Desert Locust Control Committee (DLCC) was established in January 1955 by the FAO Director-General as a global coordinating body for early warning, prevention, and management of desert locust.

The DLCC was established in accordance with Article VI of the Organization statute, with voluntary contributions from member states. The DLCC is the primary forum bringing together locust-affected countries, donors, and other agencies to discuss desert locust management under the FAO umbrella. It is a global advisory body on desert locust early warning, control, and emergencies and provides guidance to the three FAO regional desert locust commissions. In the field, the DLCC is linked by three regional commissions—CRC, SWAC, and CLCPRO—as well as by an interstate organization called the Desert Locust Control Organization for Eastern Africa (DLCO-EA). The commissions are developing a preventive control strategy by establishing autonomous national desert locust units and strengthening the national capacities of their member countries in survey, control, reporting, training, research, planning, and safety. The DLCC and the regional commissions complement each other in order to implement a complete global preventive control strategy that reduces the frequency, duration, and intensity of desert locust plagues while protecting food and livelihoods. The DLCC has 64 member states and three working languages: Arabic, English, and French.

Since 1955, from its headquarters in Rome, the FAO has operated a centralized Desert Locust Information Service (DLIS) to provide general locust information to the global community and to give timely warnings to countries in danger of invasion. The DLIS integrates information from the field with remote sensing data of meteorology, soil moisture, and vegetation in desert locust habitats. Since 1975, the DLIS has issued a monthly bulletin to locust-affected countries, the international donor community, researchers, institutes, and other interested parties that summarizes the current situation and provides a six-week forecast for each affected country. During periods of increased locust activity, the DLIS issues warnings to the affected countries and helps organize emergency control campaigns. These products are the main deliverables of the DLIS early warning system and are part of the global strategy to prevent plagues. Information provided by DLIS to National Locust Centres (NLCs) is used to plan survey and control operations in the field and prepare for swarm invasions by prepositioning resources and teams.

To promote preventive strategy and support member countries in the control of the desert locust, the FAO has established three regional commissions:

- **FAO Commission for Controlling the Desert Locust in the Western Region (CLCPRO, est. 2002)** with 10 member countries from West and Northwest Africa: Algeria, Burkina Faso, Chad, Libya, Mali, Mauritania, Morocco, Niger, Senegal, and Tunisia.
  - CLCPRO replaced CLCPANO, a past FAO commission for Northern Africa, and OCLALAV for the entire French-speaking semi-desert Sahelo-Saharan area, both now obsolete. OCLALAV was responsible for several innovations including the exhaust nozzle sprayer and the use of barrier treatments with dieldrin as an insecticide.
- **FAO Commission for Controlling the Desert Locust in the Central Region (CRC, est. 1967)** with 16 member countries: Bahrain, Djibouti, Egypt, Eritrea, Ethiopia, Iraq, Jordan, Kuwait, Lebanon, Oman, Qatar, Saudi Arabia, Sudan, Syria, UAE, and Yemen.
- **FAO Commission for Controlling the Desert Locust in South-West Asia (SWAC, est. 1964)** with four member countries: Afghanistan, India, Iran, and Pakistan.

The commissions developed a preventive control strategy by establishing autonomous national desert locust units and strengthening the national capacities of their member countries in survey, control, reporting, training, research, planning, and safety. They develop annual work plans and update their contingency plans regularly based on the situation and forecasts. In the countries that are not members of the three commissions (e.g., Kenya, Somalia, South Sudan, Uganda), the FAO works through its decentralized offices with their respective national authorities. All countries from the invasion area are members of the DLCC and are expected to be active (participate every two years in the DLCC meetings on the status of the locust situation and control mechanism, etc.). The establishment of the commissions and various field organizations has made it possible to provide logistical capacity for the development of field work, to specify the location and contours of the main outbreak areas, and to accumulate over the years a database on the seasonal location of locust populations, including their size and phase status. This database is particularly important for the desert locust and covers more than a century of field data (FAO 2022). All this has gradually led to a better understanding of the dynamics of locust populations in their natural environment, including the ecological conditions that support the development of gregarious populations in the outbreak areas, allowing the continuous improvement of preventive control and emphasizing the necessary complementarity between field and laboratory research.

Finally, following a decision by the FAO's governing bodies, the Emergency Prevention System for Transboundary Animal and Plant Pests and Diseases (EMPRES) was established in 1994 to enhance world food security and fight transboundary animal and plant pests and diseases. The desert locust component of the program provides international governance of this natural hazard: striving to enhance its efficacy, develop early warning plans, and supply sustainable emergency funds for the 18 locust-affected countries in Africa and the Near East. The program also promotes environmentally sound control technologies and close collaboration with affected countries, national and international agricultural research centers, and other international organizations.

Strategy at FAO headquarters to deal with desert locust emergencies

When desert locust populations are low, during recessions or localized outbreaks, all control operations are implemented by NLCs. When populations are high and become widespread, during upsurge and plague, NLC treatments are joined by those organized by regional organizations under the aegis of the FAO with international assistance and donor funding. In a desert locust emergency, when a preventive strategy is no longer sufficient, the FAO HQ sets up the Emergency Centre for Transboundary Plant Pests (ECTTP). ECTTP integrates technical and operational capacities under the management of the directors of the Plant Production and Protection Division (AGP) and the Food Chain Crisis–Emergency Management Unit (FCC-EMU) of the Emergency and Resilience Division (PSE) operationally managing the response. Depending on the demonstrated scale, complexity, urgency, capacity to respond, and reputational risk, the FAO Thematic Scale-Up L3 protocols applicable to desert locusts can be activated. The ECTTP monitors the desert locust with procurement, human resources, resource mobilization, and communications/outreach. It meets twice a week and issues weekly media talking points, which produce a comprehensive reflection of all issues related to the emergency. Based on the need assessment, ECTTP launches calls for resource mobilization and follow-up negotiations with donors.

Mechanism of funding for desert locust control

From 2003–2005, during the locust upsurge in the Western Region, 13 million hectares were treated with 13 million liters of pesticides in over 20 countries, and the total cost of the campaign, including food aid, exceeded USD 500 million (Brader et al. 2006). On this occasion, dysfunctions in the international pest prevention system became apparent, and the ways in which international assistance was involved were questioned (Doré et al. 2008). Donor country representatives readily admitted to having intervened too late but also held FAO and national experts responsible for the late involvement of donor organizations. The FAO's coordination skills were also questioned at the time (Doré 2010). The FAO then developed a new financial governance system for locust control (Deshormes 2011; Fig. 3). This was approved by all three desert locust commissions. Each commission applied this system, with some modifications, to the locust-affected countries in their region. The funding system approved in the Central Region consists of seven tools aligned with the four stages of locust infestation (recession, outbreak, upsurge, and plague), among them the regional emergency fund. The main feature of the system is the presence of complementary and continuous sources of funding at the national, regional, and international levels for control operations. Depending on the scope and severity of the desert locust infestation, funding for control comes from different sources (Deshormes 2011; Fig. 3). Such a scheme was in place for the desert locust emergency in East Africa in 2019–2020.

Common visions

Visions for effective locust and grasshopper management include several recurring themes. International collaboration emerges as a cornerstone, with a strong emphasis on forging partnerships between regions, countries, and international organizations. This collaboration aims to bolster sustainable management practices, advocating for preventive strategies, biocontrol methods, and the adoption of technologies such as drones, molecular tools, and advanced forecasting systems. Central to these efforts is a foundation in scientific research and transdisciplinary studies, guiding informed decision-making and robust frameworks. Challenges posed by politically insecure regions underline the need for tailored solutions, while community engagement and education are highlighted as pivotal for understanding and maintaining existing systems that work well. Moreover, the establishment and fortification of regional commissions and support from international bodies, notably the FAO, are crucial elements in this comprehensive approach. Ultimately, the collective pursuit aims for a sustainable, environmentally friendly, and technologically supported management system that addresses challenges while fostering collaboration, innovation, and expertise development.

Themed discussions

Locust biology

Evolution, behavior, and physiology of locust phase polyphenism

By Darron A. Cullen, Arianne Cease, Bert Foquet, Rick Overson, Mira Word Ries, Hojun Song, Jacob P. Youngblood, Stephen M. Rogers

Background.—As our current knowledge of the behavior, physiology, and evolution of locusts has been reviewed relatively recently (Pener and Simpson 2009, Cullen et al. 2017), we have limited ourselves to a short overview of some of the developments made since then. There are 19 species of grasshoppers considered true locusts in that they exhibit extreme density-dependent phase polyphenism and form large, dense groups of migrating individuals (Song 2011, Cullen et al. 2017, Ayali 2019). Because phase polyphenism has evolved independently several times across the family Acrididae (Song 2011, Song et al. 2017), often under different

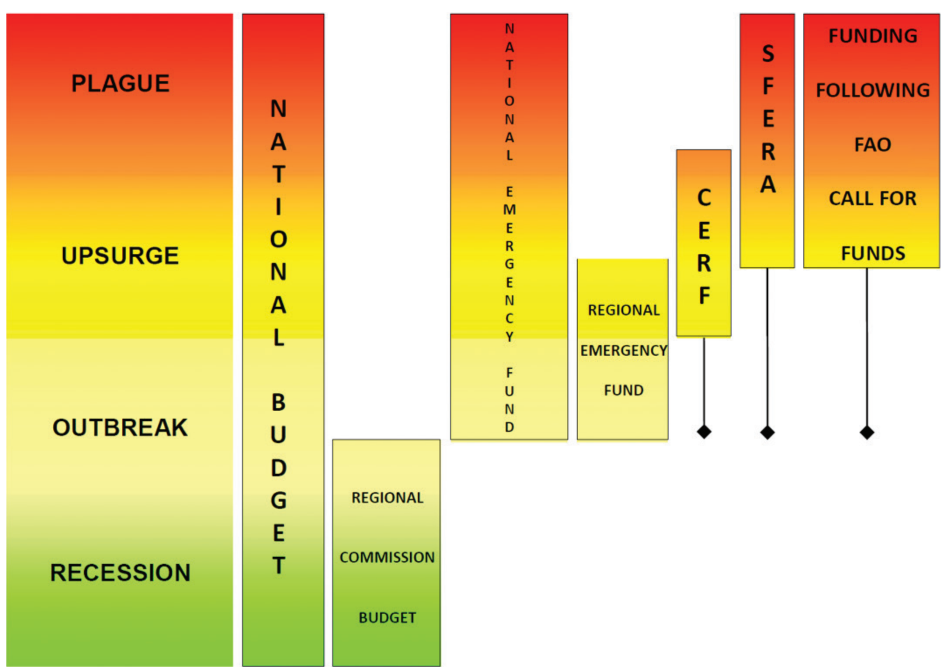

Fig. 3. FAO Desert Locust control funding scheme. CERF: UN Central Emergency Response Fund. SFERA: FAO Special Fund for Emergency and Rehabilitation. Symbol **in black (square with a vertical line above)** indicates the state of alert phase of the financial instrument in case of the predicted worsening of the situation.

environmental pressures, each locust species is expected to have evolved its own unique mechanism to undergo phase transition. Even though a detailed analysis of behavioral phase change has only been performed for four locust species (*Schistocerca gregaria*, *Schistocerca piceifrons*, *Locusta migratoria*, and *Chortoicetes terminifera*; Roessingh and Simpson 1994, Rogers et al. 2014, Foquet et al. 2022, Guo et al. 2011, Gray et al. 2009), these data have already shown that there are indeed large differences in the process of behavioral phase change, even within the genus *Schistocerca*. Nonetheless, all evidence suggests that phase change is induced by prolonged exposure to visual, olfactory, and/or tactile cues from conspecifics, rather than by any indirect effect of high population density or associated stressors, for each species for which this has been tested so far (Cullen et al. 2017). Ongoing work in less-studied locust species, such as the Australian plague locust (Gray et al. 2009, Cullen et al. 2010, 2012) and *Schistocerca* species (Pocco et al. 2019, Foquet et al. 2021, Foquet and Song 2021, Foquet et al. 2022), as well as in closely related non-swarming grasshoppers (Song et al. 2017, Kilpatrick et al. 2019, Foquet et al. 2021) will further broaden our understanding of how and why phase polyphenism has evolved repeatedly. Additionally, the advent of more affordable sequencing technologies has allowed us to further our understanding of the molecular mechanisms underlying density-dependent phase polyphenism in different locust species (e.g., Yang et al. 2019, Foquet et al. 2021) as well as to uncover some of the molecular regulatory mechanisms through which phase-related traits are regulated (e.g., Zhang et al. 2020, Zhao et al. 2021, Guo et al. 2020a).

Advances and challenges.—Density-dependent phase polyphenism in locusts is among the best-known examples of phenotypic plasticity in animals, and it can be easily studied in the laboratory due to the relative ease of rearing locusts, their amenability to RNAi and pharmacological treatments, and their relatively large size, which facilitates physiological experiments. Breakthroughs in locust behavioral physiology since Cullen et al. (2017) include the discovery that the volatile 4-vinylanisole, released from cuticular regions of the body (especially the hind legs) and also present in the feces, is a key aggregation pheromone in the migratory locust (Guo et al. 2020b) and serves to synchronize female maturation in this species (Chen et al. 2022). Both studies used a line of genomic knockout locusts in which an odorant receptor co-receptor (Orco35) was mutated using CRISPR-Cas9 genome editing, thereby consolidating this technique in locusts.

Advances have also been made in the understanding of sexual behavior in the desert locust; fieldwork by Maeno et al. (2021a) showed that females avoid harassment from males by occupying separate sites before attending male-dominated 'leks' to mate, while a complementary lab-based study by Cullen et al. (2022) used RNAi to show that the bright yellow color of males helps them to avoid mistaken (and potentially costly) male–male mounting.

Future molecular-based studies will be greatly aided by the recent publication of high-quality, chromosome-level genomes for both the migratory locust (Li et al. 2022) and six *Schistocerca* species, including the desert locust, the Central American locust, and the South American locust (Song 2022). There are also ongoing sequencing efforts by the United States Department of Agriculture's Ag100Pest Initiative to sequence the brown locust, *Locustana pardalina* (Lecoq and Zhang 2019), as well as the migratory grasshopper, *Melanoplus sanguinipes*. Due to these recent advances and the significant increase in available molecular data, we now better appreciate the differences between locust species, each with overlapping but differing suites of phenotypically plastic characteristics, which are controlled by distinctive and apparently species-specific physiological and molecular mechanisms (Wang and Kang 2014, Song et al. 2017, Ayali 2019, Foquet et al. 2021).

Nevertheless, there remain many open questions about the evolution, mechanisms, and maintenance of locust phase polyphenism, and we still do not understand the underlying molecular basis of this phenomenon. The Behavioral Plasticity Research Institute (BPRI) has been recently formed to address these outstanding questions. This new virtual research institute was funded by the U.S. National Science Foundation's Biology Integration Institutes Program in 2020 with the goal of radically advancing our understanding of phenotypic plasticity through biological integration by combining expertise from genomics, epigenetics, single cell genomics, neurophysiology, collective behavior, nutritional physiology, microbiology, ecophysiology, evolutionary biology, and more. The BPRI is a transdisciplinary effort involving researchers from Texas A&M University, Baylor College of Medicine, Arizona State University, Southern Illinois University Edwardsville, Washington University in St. Louis, and the USDA.

Future questions.—One major objective of locust research is to develop a coherent picture of how and why phase change occurs. Understanding how multiple evolutionarily conserved mechanisms of neuronal and physiological plasticity have been co-opted to produce a suite of phenotypically similar features common to phase change across locust species is an ongoing task. Even though the available data have undoubtedly expanded, there is a clear need for the following:

1) Collaborative efforts to sequence and annotate genomes for more locust and related grasshopper species, to be well integrated with functional characterization and physiology research to understand the mechanisms that produce different phenotypes;
2) Integration and relation of information across levels of biological organization from single cell to organ systems, and from organism to population, both within and between species;
3) Computing infrastructure and data repositories to manage big data; and
4) Comparative studies (cross-discipline, cross-taxon, multiscale, etc.) to maximize the impact and reach of the research.

These efforts must harness the collective person power of multiple research teams and organizations around the globe and will require established pipelines for communication and dissemination (see below).

Transdisciplinary opportunities.—Working in interdisciplinary and cross-sectoral teams should provide new opportunities for collaboration, particularly between laboratory-based researchers and stakeholders working with locusts in the field. Indeed, a particular challenge is translating insights gained from highly controlled laboratory experiments into ecological settings and exploiting these insights in locust control. Unfortunately, laboratory experiments are rarely complemented by follow-up work in a natural setting largely because lab-based researchers and wild locust populations are often on different continents. In addition, it is hard to plan field work on locust swarms due to the long absence and unpredictable resurgence of such swarms in any specific area, and often locusts swarm in inaccessible areas. Not only can collaborations between local stakeholders and locust researchers resolve this discrepancy and help researchers, it will also allow for an easier translation of fundamental locust research to locust control measures. Some research programs could also extend to further control strategies in the field, including work into the lethality of *Metarhizium* spp. and *Paranosema locustae* (synonyms: *Antonospora locustae, Nosema locustae*) (Henry and Oma 1981, Lange et al. 2000, Lomer et al. 2001, Zhang and Hunter 2017, Zhang et al. 2019) in a broader range of locust species.

Alongside the ongoing work into phase polyphenism and swarming behavior, locusts are a useful model for other questions in neurobiology (Burrows 1996, Rogers et al. 2007, Blackburn et al. 2010) and physiology (Harrison 1997, Wynant et al. 2014, Holtof et al. 2019), with most research making use of the two established laboratory locust species, *S. gregaria* and *L. migratoria*. It, therefore, seems likely that increased access to other locust species from the field would allow a further comparative aspect to many of these university-based projects, in addition to a deeper understanding of phase change in the model species.

Key review and synthesis articles.—Cullen et al. (2017), Pener and Simpson (2009)

Locust ecology and global change

By Arianne Cease, Dan Johnson, Douglas Lawton, Marion Le Gall, Rick Overson, Brittany F. Peterson, Cyril Piou, Mira Word Ries

Background.—

Organismal biology. Organismal biology typically focuses on an organism's interactions with abiotic factors in the environment and thus can also fall under the fields of environmental physiology and/or physiological ecology. Humidity and temperature are two key abiotic factors that are well studied in locusts. Many, but not all, locust species prefer hot and dry climates (Le Gall et al. 2019), and some species can thrive in extreme environments, such as the desert locust, *S. gregaria*, in the Sahara Desert (Maeno et al. 2021b). Humidity and temperature can affect color change (Pener and Simpson 2009), development (Gregg 1983), and susceptibility to pathogens (Bateman et al. 1993, Thomas and Jenkins 1997). Substantial research on thermoregulation and thermoregulatory behavior in locusts has shown temperature to be a key factor in determining survival, microhabitat choice, antipredator defense strategy, and digestion and nutrient assimilation efficiency (Miller et al. 2009, Coggan et al. 2011, Maeno et al. 2019, 2020a, 2021b, Youngblood et al. 2020, 2022, Piou et al. 2022). Rain and humidity play a crucial role in the life cycle of a locust, from oviposition (egg laying), egg development, diapause/quiescence, and susceptibility to pathogens to survival and successful migration, which are dependent on the presence of ephemeral green vegetation (Gregg 1983, Hunter 1989, Hunter-Jones 1964, Kambule 2011, Wardhaugh 1980, Woodman 2010a, 2010b). The trajectory of an organism's life is predicated on these fundamental abiotic factors being favorable enough for it to grow, avoid predators, forage, and reproduce.

Locusts and grasshoppers have been used extensively to study foraging behavior and nutrition (Bernays and Bright 1993; Simpson and Raubenheimer 2012). Grasshoppers are one of the few insect generalist herbivores that move between and eat from many different host plants (Uvarov 1977). Many factors affect foraging behavior and plant selection, including plant mechanical and chemical defenses, nutrient acquisition, and predator avoidance (Bernays and Chapman 1973, Behmer 2009, Schmitz et al. 2010, Raubenheimer and Simpson 2018). Interestingly, there are interactive effects of plant structure and temperature on the relative extraction of macronutrients from plants (Clissold et al. 2013, Clissold and Simpson 2015, Brosemann et al. 2023). Macronutrient content and balance, especially protein and carbohydrates, are strong drivers of food selection because these nutrients make up most of an herbivore's diet, and an imbalance decreases growth, survival, and reproduction (Simpson and Raubenheimer 2012). Since the 1980s, locusts have been used as a model to develop the Geometric Framework for Nutrition (Raubenheimer and Simpson 1993). This has brought insights into the effect of phase on foraging behavior (Simpson et al. 2002, Zee et al. 2002, Despland and Simpson 2005), the effect of marching on carbohydrate hunger (Cease et al. 2023), and the effect of food resources on gregarization (Despland and Simpson 2000) and migration (Cease et al. 2017). More recent nutritional work merges lab and field research by studying field populations of locusts. This research has demonstrated that, in contrast to the common idea that herbivores should be nitrogen and protein limited (Andrewartha 1954, White 1993), many locusts prefer and grow best in low-nitrogen environments harboring plants with low protein and high carbohydrates (Le Gall et al. 2019). This relationship between low nitrogen plants and/or high carbohydrate plants and locust outbreaks has been shown for the Mongolian locust, *Oedaleus decorus asiaticus* (Germar, 1825), in China (Cease et al. 2012), the Senegalese grasshopper, *Oedaleus senegalensis*, in Senegal (Le Gall at al. 2020a, Le Gall at al. 2020b, Word et al. 2019), the Australian plague locust, *C. terminifera*, in Australia (Lawton et al. 2020, 2021), and the South American locust *S. cancellata* in Argentina, Bolivia, and Paraguay (Talal et al. 2020, Trumper et al. 2022). These studies have revealed a consistent high demand for carbohydrate-rich diets by outbreaking populations, likely due to high energy demands and possibly to support lipids for egg production and survival in an arid environment (Cullen et al. 2017).

Populations: The study of locust populations includes population dynamics, range distributions, gene flow, and local adaptation. The growth of local grasshopper and locust populations can be limited by the availability of resources (bottom-up control), predators, or pathogens (top-down control), as well as emigration and immigration. Because locusts often live in arid environments, they follow the pulse resource paradigm, with outbreaks heavily influenced by preceding green vegetation (Lawton et al. 2022). In addition to plant availability, plant quality (nutrients and plant defenses) can affect population growth. Thus, factors such as flooding, drought, fire, atmospheric CO_2, and livestock grazing that influence plant quality and many other ecosystem factors affect growth, survival, and overall population dynamics (as shown in grasshopper populations: Joern and Gaines 1990, Joern et al. 2012, Lenhart et al. 2015, Branson and Vermeire 2016, Branson 2017, 2020, Welti et al. 2020). In temperate zones, particularly northern regions with seasonal cold and warm periods, development and population growth are limited by heat requirements, at first through soil temperature and resultant egg hatching and later through insolation and environmental heat as it drives development (Lactin et al. 1995, Lactin and Johnson 1998, Brust et al. 2009). The magnitude of impact from these factors likely varies throughout an outbreak cycle and across different environments. Unlike low-density solitarious populations, predation is thought to have a limited impact on high-density gregarious locust populations because their population numbers increase much faster than their predators (Farrow 1982). Thus, individual locusts confer a benefit from being part of the crowd when at high density as they are less likely to be eaten. Environments with higher moisture levels likely leave xerophilic locusts that prefer open arid areas more susceptible to pathogens (Arthurs and Thomas 2001). Habitats with more complex plant architecture (e.g., forests as compared to grasslands) may increase predation by harboring more vertebrate natural enemies and hampering escape flights by locusts (Clark 1950, Lawton et al. 2020). These vulnerabilities may explain, in part, why desert and grassland locust species tend to avoid woody vegetation (Deveson and Hunter 2002), become most abundant in arid environments (COPR 1982) and tend not to persist long-term in more mesic zones when they do invade.

Due to their migratory capacity, often high local abundance, and large geographic ranges, locust species are generally predicted to avoid strong population bottlenecks in evolutionary time, have high levels of gene flow, large effective population sizes, and high overall genetic diversity. These predictions have generally been supported by the handful of population genetic studies on locusts. Analysis of genetic markers across the range of the Australian plague locust demonstrated very high overall genetic diversity, extremely large effective population sizes, and a remarkable lack of population structure across the continental range of the species (Chapuis et al. 2011). Similarly, Chapuis et al. (2014) found that the highly migratory desert locust exhibited high genetic diversity overall and low genetic structure across recently solitarized populations during a recession period, suggesting that solitarious populations are not isolated or, if drift and selection do act to differentiate isolated populations after plagues subside, they do so slowly. In the widespread and highly mobile migratory locust, *L. migratoria*, the pattern is more complex. The species also exhibits high levels of gene flow and low structure across continental scales like the desert locust, but evidence of genetically distinct subpopulations have been detected that correspond to particular regions (see Chapuis et al. 2008, Chapuis et al. 2017, 2014, Zhang et al. 2009a, Ma et al. 2012). Sufficiently high levels of gene flow can erode the genetic signal of animal movement, making it challenging to understand migration patterns through a population genetic approach (Chapuis et al. 2011). Interestingly, high gene flow and low inter-population structure could play a role in locust boom-and-bust population dynamics. During population booms, locusts temporarily expand their range into novel habitats but often fail to persist in these areas. The high measured gene flow in locusts will effectively erode any advantageous local adaptation across heterogeneous and novel environments (Storfer et al. 1999). Understanding the metapopulation dynamics of locusts can both inform management approaches and lead to a better understanding of the selective pressures leading to the evolution of phase change and swarming behavior.

Communities: Community ecology focuses on the interactions among different species living in the same area, such as competition, predation, and mutualism. These interactions can be moderated indirectly through host plants, natural enemies, and physical factors (Denno et al. 1995, Kaplan and Denno 2007, Smith et al. 2008). For example, species in a community with overlapping diets may directly compete for host plants (Schoener 1982); however, the situation is often more nuanced. One explanation for the coexistence of generalist herbivores is the nutrient niche hypothesis (Lenhart 2014). Behmer and Joern (2008) revealed that several species of grasshoppers from the genus *Melanoplus* selectively feed to achieve unique ratios of protein and carbohydrate as late juveniles, potentially filling different nutritional niches even if they eat the same plant taxa.

Common predators of locusts and grasshoppers include beetles, wasps, flies, spiders, lizards, frogs, coyotes, birds, ants, and parasitoids such as hairworms (Nematomorpha), parasitoid wasps, and parasitoid flies (Martin et al. 1998, 2000, Danyk et al. 2000, Johnson et al. 2002, Biron et al. 2005, Shi et al. 2019, Mullié 2021). Predatory natural enemies, such as beetles, are important vectors for microsporidian diseases like *Paranosema locustae*, whose spores are present in predators and other organisms in the community, therefore providing additional sources of infection for grasshoppers besides their own horizontal transmission (Shi et al. 2018a). See the population section for more discussion on how predation affects locust population dynamics.

Commensal or beneficial microbial communities have the potential to impact locust ecology and behavior. Recent locust microbiome research has illuminated the gut bacterial community composition and symbiont-mediated processes within the host (Stoops et al. 2016, Garofalo et al. 2017, Lavy et al. 2019, Lavy et al. 2020a), though efforts to understand the interactions with and influence of the microbes associated with locusts have been limited to relatively few species (recently reviewed in Lavy et al. 2020b). To date, desert locust symbionts are among the best characterized. Desert locust-associated bacteria were first shown to impact their host's pheromone production and aggregation (Dillon et al. 2000, Dillon et al. 2002). Importantly, differences in the bacterial community structure in the gut have been observed regarding food availability, age, and phase (Dillon et al. 2010, Lavy et al. 2019, Lavy et al. 2022). Lavy et al. (2022) showed that high-density rearing conditions in the lab led to horizontal transmission of *Weissella* (Firmicutes); this led the authors to hypothesize that this bacterium may play a critical role in aggregation and phase change. The structure and diversity of female reproductive tract bacteria have also been correlated with host phase in the desert locust (Lavy et al. 2021), and some gut bacteria are passively transmitted via the foam plug from mother to offspring (Lavy et al. 2021). Gut microbiota can heavily influence locust interactions with potential pathogens. For example, *P. locustae* alters the gut community composition during infection of the migratory locust (Tan et al. 2015), and tolerance to the opportunistic pathogen *Serratia marcescens* is conferred by gut bacteria in the desert locust (Dillon et al. 2005).

Ecosystems: Ecosystem ecology looks at interactions among biotic and abiotic components and tends to focus on flows, fluxes, and processes. While locust outbreaks are mostly viewed as negative due to their impacts on aboveground biomass, the actual and potential benefits of locust swarms are rarely acknowledged. Locusts are typically not pests from an ecological or evolutionary context. Indeed, locusts and grasshoppers play important roles in ecosystem structure and function through their contribution to trophic dynamics, nutrient cycling, stimulating plant growth, and biodiversity (Gandar 1982, Kim 1993, Schmitz 1994, Belovsky and Slade 2000, Guo et al. 2006, Fielding et al. 2013, Descombes et al. 2020, Kietzka et al. 2021).

Herbivores transfer energy from plants directly to decomposers via plant clippings, feces, and cadavers. By changing the abundance and decomposition rate of plant litter, grasshoppers may speed up nitrogen cycling and can increase plant abundance in some ecosystems (Belovsky and Slade 2000). On a larger scale, the ecological effects of locust outbreaks are largely unstudied. A swarm of locusts redistributes nutrients hundreds of kilometers away from the soil where the plants they damaged grew. This makes them important transporters of nutrients, especially in arid nutrient-poor ecosystems. The effect a locust swarm has on nutrient cycling depends on the quantity of nutrients in frass or cadavers and on the time it takes for those nutrients to become available to plants. Kietzka et al. (2021) calculated that nitrogen mineralized from the frass and cadavers of a 1 km^2 area (100 ha) of locusts and their offspring could meet the nitrogen requirements of around 306 ha of rice crops and 59 ha of maize plants. Although logistical hurdles remain, with a shift in perspective locust outbreaks could be more sustainably integrated into regional food systems by using them as fertilizer, fodder for livestock, and a nutritious source of protein, minerals, fat, and fiber for humans (Kietzka et al. 2021).

Landscapes and technology: Landscape ecology focuses on spatially explicit interactions between biotic and abiotic components across scales. The scale of locust distribution, aggregation, and movement across heterogeneous landscapes makes landscape ecology an important research approach. Indeed, determining locust ecology and distributions is foundational for monitoring, management, and forecasting (e.g., Italian locust, *Calliptamus italicus*; Sergeev 2021a). The occurrences of different locust and grasshopper species tend to be correlated with different biomes (e.g., across Eurasia; Sergeev 2021b) and quite sensitive to heterogeneity in land cover. On-the-ground studies that directly measure landscape features simultaneously with species' traits across large regions are uncommon, perhaps due to challenging logistics, but are important for understanding unexpected patterns such as the interactive effects of precipitation gradients and land use (Hao et al. 2015), how different species respond to changing nutritional landscapes (Lawton et al. 2021), degrees of plant specialization across a climatic gradient (König et al. 2022), and differences in behavior and growth rates in heterogeneous anthropogenic landscapes as compared to semideserts (e.g., Italian locust; Sergeev and Van'kova 2008). Smaller-scale studies can simultaneously test the effect of multiple top-down and bottom-up factors affecting locust distribution (e.g., Australian plague locust; Lawton et al. 2020). Field sampling within the Central American locust gregarization zone revealed stronger correlations with vegetation, land use, and climatic factors than soil characteristics for this species and that the biomass of *Panicum maximum* grass was especially positively correlated with locust density (Poot-Pech et al. 2018). Tracking migration across landscapes is logistically challenging, but swarms can be monitored using radar and remote sensing (Drake 1983, Drake and Farrow 1983, Drake et al. 2002, Deveson et al. 2005, Hao et al. 2017), and inferences can be made based on where swarms are recorded over time (Berg 2021) and/or where specimens are found (Giuliano 2021). While locusts can migrate over many types of habitats, successful breeding areas are usually restricted to areas with a combination of favorable soil and climatic conditions, generally referred to as "outbreak areas" (Showler et al. 2021). Thus, predicting breeding and gregarization sites is important to inform monitoring efforts, especially for the desert locust due to its vast recession zone (Kimathi et al. 2020). The spatial distribution of resources can provide clues as to high-risk gregarization sites as they affect locust aggregation and phase change (Collett et al. 1998, Despland et al. 2000, Despland and Simpson 2006, Georgiou et al. 2021). An understanding of landscape ecological processes is important for improving spatiotemporal risk forecasting tools at different levels of risk (Piou and Marescot 2023).

New technologies have fueled major advances by facilitating large-scale approaches. The first use of PC-based geographic information systems for managing insect survey data and forecasting insect outbreaks was for grasshoppers (Johnson and Worobec 1988, Johnson 1989a,b). The advent of satellites, specifically LANDSAT in the early 1970s and MODIS in 2000, paved the way for comparisons between the normalized difference vegetation index (NDVI, a measurement of vegetation greenness) and outbreaks (e.g., McCulloch and Hunter 1983, Despland et al. 2004, Deveson 2013, Drake and Wang 2013, Piou et al. 2013, Lawton et al. 2022). Remote sensing collects information over large geographical areas and relays surface conditions back to specialists, enabling them to visualize data in near real time (Latchininsky and Sivanpillai 2010, Klein et al. 2021). For example, detecting soil moisture estimates at a 1 km resolution can be used to plan preventive management and other integrated pest management strategies (Piou et al. 2019). Advances in remote sensing aid in habitat monitoring and risk assessment for prominent species, such as the desert and Australian plague locusts, but are unused for many other species. Widespread implementation of remote sensing for locust management and on-the-ground verification for research is often thwarted by the remote locations of locust habitats and a distribution range that spans across countries (Latchininsky 2013). Furthermore, new satellites often belong to private commercial operations and can be costly to access. Most remote sensing research has focused on the desert locust (Despland et al. 2004, Renier et al. 2015, Waldner et al. 2015), migratory locust (Shi et al. 2018b, Geng et al. 2020, 2022, Zhao et al. 2020), and Australian plague locust (Deveson 2013, Lawton et al. 2022). There are new remotely sensed sources that give even finer spatial resolution and temporal scales. For example, the Sentinel program has been flying since 2015 and can provide NDVI estimates at 10 m^2 pixel resolution and a five-day return time. In the private sector , there are numerous technology companies focusing on even finer spatial resolution imagery. These technologies should be considered going into the future.

Drones have been given significant attention for advancing locust research and management with the hope of expanding survey areas, transmitting landscape images to decision-makers in real time, and actual spraying during control campaigns. At present, drones are mainly used to aid in the surveillance of remote areas. Recent success was seen with a drone developed by HEMAV in 2020 for countries impacted by the desert locust (Matthews 2021). Their dLocust drone can process images in flight, making data immediately available to decision-makers using the eLocust3 tablet at the end of its long-distance survey (Matthews 2021). However, drones are limited in the weight they can carry for control spraying (only 10 kg), battery life (limiting flight time to 10–15 min), battery expense, operating costs, and lack of trained operators (Matthews 2021). Drones must be affordable, simple to operate, and easy to maintain in locust-affected countries. Additionally, aviation regulations that require operators to keep their aircraft within visual line of sight may be prohibitive for long-distance flights (Cullen et al. 2017). More research and development are needed to create the most effective designs, standard operating procedures, and safe and effective ways drones can be used in locust control (Ochieng' et al. 2023).

Much of the technology mentioned above is being influenced and enhanced by individual people and their smartphones. Applications such as the Food and Agriculture Organization of the United Nations' (FAO) eLocust3m, which was launched in 2015, can be used by community members, farmers, and control officers to record locust sightings and help with monitoring and forecasting efforts. Apps can use machine learning to identify, with some accuracy, locust species, among other pests, and transmit data in real time to national locust centers and relevant personnel. With the increased quality and quantity of survey points in georeferenced databases, it is possible to relate pest and vegetation status to the density threshold of populations that may lead to gregarization (Cissé et al. 2013). This can then be used by survey teams as an additional indicator of risks (Cissé et al. 2016). Further studies are needed to relate the hopper density threshold of gregarization to vegetation (Cissé et al. 2015) and to verify these relationships for other species. These georeferenced databases are also useful for actualizing maps of habitat use, reproduction, and gregarization (e.g., Piou et al. 2017, Kayalto et al. 2020) or understand population dynamics in relation to environmental drivers (e.g., Lazar et al. 2016). Halubanza et al. (2022) identified machine learning as a solution to a dearth of identification skills. However, it is likely that skilled human diagnosticians will continue to be a crucial component for the rapid identification of large numbers of insects and dealing with imperfect specimens.

Global change: Global environmental change is among the most pressing challenges we face today (IPCC 2022). Climate and land-use/land-cover change (LUCC) have substantial direct and indirect impacts on locust and grasshopper populations, although the directionality and extent are not well understood due to the complexity of interacting factors (Meynard et al. 2020, Oliver and Morecroft 2014). Although our understanding of locust range dynamics lags far behind that of other insects of management concern (e.g., the yellow fever mosquito, *Aedes aegypti*; Kearney et al. (2009)), we know some locust and grasshopper species are predicted to shift their distribution range in response to climate change (Guo et al. 2009, Meynard et al. 2017, Youngblood et al. 2022), change their gregarization areas (Kayalto et al. 2020), and outbreak potential (Yu et al. 2009, Olfert et al. 2011, Latchininsky 2017) while others could decrease (Wang et al. 2019) or fail to expand to new regions due to lack of winds favoring migration (Wang et al. 2020). The outbreak range of the South American locust (*Schistocerca cancellata*) is predicted to expand to higher latitudes and altitudes (Youngblood et al. 2022), while that of the Australian plague locust is predicted to contract (Wang et al. 2019). Solitarious ranges of the two desert locust subspecies are predicted to have contrasting responses; while the well-known northern subspecies (*S. gregaria gregaria*) range may contract in some areas, the lesser studied southern subspecies (*S. gregaria flaviventris*) range is predicted to expand (Meynard et al. 2017). This research highlights that while *S. g. flaviventris* has only rarely had outbreaks historically, it is a subspecies that may pose a future threat.

Due to their mobility, herbivores shift to higher elevations faster than plant communities do, thus disrupting the ecological relationships between herbivores and plant communities (Descombes et al. 2020). In areas where temperatures and rainfall increase, stronger wind and tropical cyclones (e.g., the North Indian Ocean) may create favorable environments for locust breeding and migration (e.g., desert locusts in the Arabian Peninsula) (Salih et al. 2020; Peng et al. 2020). Elevated atmospheric carbon dioxide can have indirect effects, such as increasing plant growth and diluting plant nitrogen content, which will have different effects based on locust species and habitat, although long-term ecological datasets are important for uncovering these correlations (Welti et al. 2020). Recently generated microclimate data, including temperature, wind speeds, and soil temperature (Levy et al. 2016, Kearney et al. 2019), and modeling tools (e.g., NicheMapR; Kearney and Porter 2020) have further assisted with predicting the effects of environmental change on the behavior, distribution, and abundance of grasshoppers and other organisms (Maeno et al. 2021b). Additional recent modeling tools also include spatial point pattern analysis (SPPA) (Poniatowski et al. 2020) and machine learning (e.g., MaxEnt; Saha et al. 2021). Modeling frameworks that consider how climatic variables will impact biopesticide effectiveness can also be helpful in providing management guidelines for practitioners (Kamga et al. 2022).

The favorable habitat area for the migratory locust in China decreased and shifted from 2000 to 2020 in response to land use and land cover change (Zhao et al. 2020). Conversions to grassland, cropland, and wetland from woodland and artificial surfaces, such as concrete, increased locust habitat, whereas conversions in the opposite direction decreased them. Similarly, deforestation has likely led to locust outbreaks and swarms of the migratory locust in Australia (Farrow 1979) and Indonesia (Lecoq and Sukirno 1999) and of the Central American locust (Poot-Pech 2016, 2017). In addition, the expansion of pastures from deforestation and locust outbreaks is linked to land management practices that degrade soils and lower plant nitrogen content, such as continuous high livestock grazing (Cease et al. 2012, 2015, Medina et al. 2017, Word et al. 2019, Le Gall et al. 2020a). In Senegal, the Senegalese grasshopper, *O. senegalensis,* a non-model locust, has been found to be most abundant in field cropping systems with low soil organic matter and plants with low nitrogen and protein and high carbohydrate contents (Le Gall et al. 2020b, Word et al. 2019), which matched its preference for low protein, high carbohydrate diets (Le Gall et al. 2020a,b). In Paraguay, South American locusts have been found to perform best on invasive grasses with high carbohydrate content (Talal et al. 2020). Similarly, in China, pastures degraded by heavy livestock grazing promoted outbreaks of *O. decorus asiaticus* by lowering nitrogen and creating an optimal nutritional niche for the species (Cease et al. 2012).

Advances and challenges.—Comparative studies of locust species, particularly non-model locusts, continue to be challenging because of the geopolitical context of many locust outbreaks. On the other hand, modern outbreaks, like that of the South American locust (2015–2021) and the desert locust (2019–2021), have the potential to inspire new ecological insights (e.g., for the South American locust, Talal et al. 2020, 2021, Trumper et al. 2022, Scattolini et al. 2022) and partnerships as well as funding opportunities for much needed field-based ecological research (Medina et al. 2017, Liu et al. 2021, Samejo et al. 2021). Field control treatments have been monitored for non-target effects on natural enemies and wildlife (Martin et al. 1998, Mullié et al. 1991, Mullié 2021, Smits et al. 1999). Molecular tools have supported advancements in the study of the population genetics of locusts (Blondin et al. 2013, Yassin et al. 2006) and in characterizing their associated microbes (Lavy et al. 2018, 2020a,b, 2021, 2022). Additional advancements have been made studying gregarious behavior in field populations (Buhl et al. 2012, Cissé et al. 2013, Maeno et al. 2020b, 2021a).

Locusts and grasshoppers have been a model for foundational nutrition studies for decades (Simpson and Raubenheimer 2012, Joern 1990, Behmer 2009). Building on this research, the past decade has brought advances in uncovering interesting interactions of nutrient acquisition and cycling with temperature (Clissold et al. 2013, Clissold and Simpson 2015), predation (Leroux et al. 2012), and migration (Cease et al. 2017). Extensive field work has expanded the largely lab-based nutrition and plant-insect interaction research into a broader ecological context globally, including in Asia (Cease et al. 2012, 2017, Gui-He et al. 2013, Zhang et al. 2014, Huang et al. 2017, Li et al. 2019), the South Pacific (Graham et al. 2015, Lawton et al. 2020, 2021), Latin America (Poot-Pech et al. 2016, 2018, Talal et al. 2020), and Africa (Moussi et al. 2011, Cissé et al. 2013, Touré et al. 2013, Le Gall et al. 2020a,b, 2021, 2022, Word et al. 2019). These studies have brought into sharp relief the connections between soil, plants, land use practices, and locust populations (reviewed in Le Gall et al. 2019 and Cease et al. 2015) and explored the role of locusts distributing nutrients across ecosystems (Kietzka et al. 2021).

Rapid development and expansion of technology for collecting and processing remotely sensed data combined with modeling advancements (e.g., Kearney and Porter 2020) have supported a surge of landscape and global change studies (e.g., Deveson 2013, Drake and Wang 2013, Piou et al. 2019, Latchininsky 2013, Waldner et al. 2015, Lawton et al. 2022, Wang et al. 2019, Olfert et al. 2011, Peng et al. 2020). Technology operated on the ground (e.g., drones and smartphones) is promising, but limitations remain in adapting devices to remote and harsh environmental conditions, training users, converting raw data into useful information, and integrating diverse data types into forecast models (Matthews 2021, Piou and Marescot 2023). Therefore, due to the immense complexity of the system and in integrating data for unique taxa, it remains challenging to make clear predictions about the directionality and extent of the impact of global change on locust populations (Meynard et al. 2020).

Future questions.—With accelerating global change, studies revealing the mechanisms by which abiotic and biotic factors affect locust populations and migration will be of paramount importance, particularly in determining which species or populations may pose future threats so monitoring practices can be implemented. At the organismal level, future studies should include the complexity of multiple interacting factors such as trade-offs between reproduction, migration, and immune function. Although challenging, studying the life history, behavior, and migration patterns of field populations is paramount to support population ecology models and to understand how community interactions and population dynamics are affected during outbreak and recession cycles. Understanding the metapopulation dynamics of locusts can inform management approaches and lead to a better understanding of the selective pressures that evolved phase change and swarming behavior. Future questions about the locust microbiome and how it plays a role in phase change, dietary preferences, immune response, and behavior will be of interest in community ecology. From a landscape perspective, we need to ask questions that uncover more about what limits range expansion, aggregation, and migration. More studies that compare locust species, particularly non-model locusts that are predicted to respond differently under climate change, will be of interest. While climate and land-use/land-cover change are usually considered separately under global change, they have interactive effects, and further locust research and modeling should focus on their combined effects.

Transdisciplinary opportunities.—Although there have been many field studies on most locust species (e.g., Davey 1959, Davey et al. 1964, Farrow 1975, Lecoq 1975, Lecoq et al. 2011b, Morant 1947, Popov 1959, 1965, among a multitude of other field works), they are still considered limited, particularly because of the difficulties in finding solitarious locusts in appreciable numbers, the complexity of studying locust populations in the field, and the length of time required to obtain tangible results. Yet, more field-based ecological studies are critical to ground laboratory findings in a meaningful context and provide an excellent and important opportunity for cross-sectoral collaborations and community-based participatory research. These ecological studies will benefit from more integration with genomics, transcriptomics, neuroscience, and physiology (see section "Evolution, behavior, and physiology of locust phase polyphenism") to uncover sub-organismal mechanisms that influence landscape-level outcomes. One approach could include controlled large field cage experiments in locust habitats using lab-reared insects. This interventionist approach would allow for testing key questions in nature while controlling for locust genetics, history, and population density as well as overcoming the difficulty of finding solitarious or transiens locusts in their habitat. While the number of studies that work across scales to situate locusts within a broader social-ecological system is increasing, more ecological research that incorporates social science would help empower land stewards and other stakeholders to make informed decisions based on an understanding of human norms, values, and perspectives. These transdisciplinary approaches are becoming even more imperative as global change continues to increase complexity and uncertainty. Ultimately, navigating the human social and political dynamics involved in decision-making will remain critical to implementing research findings into policy and practice.

Key reviews and synthesis articles.—Lavy et al. (2020b), Le Gall et al. (2019), Meynard et al. (2017), Piou et al. (2019), Welti et al. (2020), Piou and Marescot (2023), Cease (2024)

Locust and grasshopper preventative management and biopesticides

By David Hunter, Amadou Bocar Bal, Dan Johnson, Carlos E. Lange, Michel Lecoq, Mario Poot-Pech, Mira Word Ries, Derek A. Woller, Long Zhang

Background.—Locusts and grasshoppers often require intense treatment programs to limit damage, but too often, treatments are not initiated until populations have reached economically relevant numbers and are already damaging crops. Chemical pesticides are applied to protect crops, but even with the use of widespread application of chemicals, it can be difficult to prevent serious damage. As a result, many governments and international organizations have adopted preventive management: treatments begin before pests reach devastating levels and, whenever possible, before they reach crops. Widespread preventive management began in the 1960s and is currently advocated as an approach for reducing, or even preventing, outbreaks (Mbodj and Lecoq 1997, Hunter 2004, Brader et al. 2006, Cressman 2008, Magor et al. 2008, Zhang et al. 2019). This involves well-planned monitoring and localized treatment, particularly in suspected breeding areas where nymph (juvenile grasshoppers without fully developed wings) bands are predicted to occur. Preventive practices have been credited for decreasing the duration and scale of agricultural damage (Lecoq 2001, Brader et al. 2006, Magor et al. 2008, Sword et al. 2010, Zhang et al. 2019). Locust and grasshopper management has been reviewed recently (Cullen et al. 2017, Zhang et al. 2019), and there has been a clear recognition of the many impediments to efficient preventive population management. These impediments will be discussed both later in this section and in the sections "Social sciences" and "The humanities and ethics of locust control," where we devote additional attention to regional management practices in various parts of the world.

In the following sections, we discuss the importance of biocontrol in preventive management because of the growing interest in developing ecologically sensitive alternatives. For an early intervention to be most effective, locusts and grasshoppers must be treated *wherever* they are found, even within or adjacent to environmentally sensitive areas where chemical pesticides cannot or should not be used. Biopesticides can be used in such areas and have been important for early intervention/preventive management in Australia, Mexico, China, and elsewhere.

Paranosema locustae.—The locust and grasshopper pathogen *Paranosema locustae* belongs to the Microsporidia, a diverse group of obligate, spore-forming parasites of various eukaryotic hosts. Their evolutionary origins have been a mystery, but they are now understood to belong to a lineage that is sister to most extant fungal species (James et al. 2020). The taxon's original description by Canning (1953) placed *P. locustae* in the genus *Nosema* based on superficial similarities to the silkworm pathogen *Nosema bombycis*. More recently, two research groups independently but in parallel published data demonstrating that the taxon in question is indeed only distantly related to "true" *Nosema* (Sokolova et al. 2003, Slamovits et al. 2004). To remedy this, Sokolova et al. (2003) proposed transferring *N. locustae* into a newly erected genus, *Paranosema,* whereas Slamovits et al. (2004) proposed transferring *N. locustae* to the existing genus *Antonospora*. Subsequently, and most recently, Sokolova et al. (2005) made arguments for retaining the taxon in *Paranosema* (as opposed to *Antonospora*) citing, among other things, additional meaningful differences in morphology and genetic separation between *Paranosema* (inclusive of *P. locustae*) and *Antonospora*. Regardless, both *Paranosema* and *Antonospora* are closely related. Thus, we refer to the taxon described by Canning in 1953 as *P. locustae* throughout.

During the 1960s and 1970s, the microsporidium *P. locustae* was developed as an alternative to chemical pesticides (Henry 2017, Lange and Sokolova 2017, Zhang and Lecoq 2021). However, its slow activity (nearly three weeks), combined with low final mortality (60–70%), limited its use in the United States (Streett 1996–2000, Johnson 1997, Lockwood et al. 1999). However, *P. locustae* has been tested in the field in Argentina (Lange and Cigliano 2005), Australia, and China and has been found to persist and spread in grasshopper communities, inducing mortality over several years (Solter et al. 2012, Bjornson and Oi 2014). Conversely, in Canada, Johnson and Dolinski (1997) found that the low virulence of *P. locustae* could not be readily overcome by repeated applications, although in that large-plot replicated field study, all applications resulted in significant infection rates and reductions. In a large-plot study of early application, late application, or both, Johnson (1989c) found that double application (June and July) did not improve on one application in mid-summer. It has also been used in Cape Verde, Mali, Mauritania, Niger, and Senegal (Henry et al. 1985, Tounou et al. 2008, 2011) but with no long-term follow-up monitoring except for some limited efforts in Cape Verde and Senegal where *P. locustae* was found between 13–23 years after applications.

In addition to its persistence, *P. locustae* has sublethal effects, including reductions in fecundity, longevity, food consumption, disruption of aggregation behavior and phase change, and inactivity (Schaalje et al. 1992, Shi and Njagi 2004, Fu et al. 2010, Feng et al. 2014, Lange and Cigliano 2005), which can have important effects on populations (Jaronski 2012), as seen in Argentina where the persistence of *P. locustae* helped reduce frequency and intensity of outbreaks (Lange and Sokolova 2017, Lange et al. 2020). Johnson and Pavlikova (1986) measured reductions in the consumption of grass in large field cages in replicated plots when grasshoppers were infected with individual doses of *P. locustae.* In China, more virulent strains of *P. locustae* have been selected and produced using high-yield technologies. Large-scale field applications led to mortalities of >80% with migratory locusts (Zhang et al. 1995, Gong et al. 2003). In addition, *P. locustae* use has recently expanded into Lao People's Democratic Republic (PDR) and Vietnam against the yellow-spined bamboo locust, *Ceracris kiangsu* (Lecoq and Zhang 2019), which has caused substantial damage since 2014 (Phithalsoun and Zhang 2018). Field trials have shown that *P. locustae* used against locusts at high densities successfully suppressed the second and third instars of the yellow-spined bamboo locust (Zhang and Lecoq 2021). Conversely, crowded gregarious locusts may be resistant to *P. locustae,* as observed in gregarious South American locusts when treated en masse in the laboratory (Pocco et al. 2020).

Metarhizium acridum.—The genus *Metarhizium* includes entomopathogenic fungi, often with a narrow host range. *Metarhizium* isolates and species, discovered and identified based on anatomy, PCR DNA tests (Entz et al. 2005, 2008), and spectroscopy (Hetjens et al. 2022), have been used to develop effective biopesticides, usually applied as conidia in oil, oil–water emulsion, or powder. *Metarhizium anisopliae* was first used for insect control over a century ago in Russia (reviewed by Lord 2005). This fungus (previous synonym *M. anisopliae* var. *acridum*) has been proven to kill locusts and grasshoppers (Milner 1997) via internal infection following penetration of the insect integument. *Metarhizium* has been shown to be active against grasshoppers at relatively high temperatures (Thomas and Jenkins 1997). Research on the isolation, formulation, and efficacy testing of *Metarhizium* for microbial control of insect pests has been conducted for over a century, including in recent decades for locust control (Lomer et al. 2001, Hunter 2004). Commercial products of *Metarhizium* are mass-produced on solid, semi-solid, or liquid substrates (Wu et al. 2014), and the use of *Metarhizium* for grasshoppers and locusts is environmentally sustainable and effective. *Metarhizium acridum* (used mainly in Africa and Australia) and *M. brunneum* (South America, North America, China, and others) have much lower virulence to insects in other taxonomic orders and no virulence to birds via contact, consumption of conidia, or consumption of infected grasshoppers (Johnson et al. 2002). Therefore, *M. acridum* is particularly useful for treating environmentally sensitive areas, organic farms, and locations in which landholders are about to send their animals or crops to market (Hunter 2004).

Research on *M. acridum* began following the large plague of the desert locust in the late 1980s. After screening many African isolates for virulence within the framework of the Lutte Biologique contre les Locustes et les Sauteriaux (LUBILOSA) international project, the IMI8033 isolate of *M. acridum* was tested in laboratory and field trials and found to be the most effective (Lomer et al. 1993, Greathead et al. 1994, Langewald et al. 1997). From this, a commercial product, Green Muscle®, was developed by the late 1990s. In Australia, an *M. acridum* isolate collected from a spur-throated locust, *Austracris guttulosa* (Walker, 1870) (Lecoq and Zhang 2019) in the Queensland tropics was developed as Green Guard® by the Commonwealth Scientific and Industrial Research Organisation (CSIRO), and in 2000–2001, the Australian Plague Locust Commission (APLC) treated nearly 25,000 ha of locust bands, the first operational use of *M. acridum* in the world (Milner 1997, Hunter 2004, Zhang and Hunter 2005). In Brazil, the use of *M. acridum* to control locusts was considered as early as 1993. Studies conducted by the Brazilian Agricultural Research Corporation (Embrapa) until 2006 focused on the production, formulation, and field evaluation of the efficacy of a local strain of *Metarhizium* and the effects on non-target insects. This mycopesticide showed high efficacy on the Mato Grosso locust, *Rhammatocerus schistocercoides*, but never reached an operational stage (Magalhães et al. 2000, Magalhães and Lecoq 2006).

Trials were also conducted with *M. acridum* in Mexico (Hernández-Velásquez et al. 2003, Barrientos-Lozano et al. 2005) and in China (Zhang and Hunter 2005), with both Green Guard® and local isolates. In Mexico, a local *M. acridum* product has been incorporated into treatment programs for the Central American locust and is applied as barrier treatments, either by air as ultra-low volume (ULV) (2,000–4,000 ha per year) or by ground (50–350 ha). The results of aerial applications have been successful, and in some areas where *M. acridum* has been applied, the locust populations have remained low for several years (Poot-Pech and García-Ávila 2019). These treatments can prevent swarm formation in ecological reserves and in areas of honey production to avoid the high risk of chemical pesticides to both bees and other non-target organisms.

In China, local production has kept the price similar to that of chemical pesticides, and the use of ULV formulations and proper application techniques ensures a high level of mortality (Zhang and Hunter 2005, Ding and Zhang 2009, Zhang 2011). As a result, biopesticides form a substantial part of locust and grasshopper population management with about 100,000 ha treated each year (Zhang and Hunter 2017). However, Li et al. (2023) identified four main reasons—very similar to obstacles in other regions—as to why biopesticides are still not used more extensively than they are currently to manage locust outbreaks in China: perceptions that biopesticides are costly, less effective, not available in markets, and that field application is difficult.

There have been applications of *M. acridum* during specific campaigns under the supervision of the FAO in East Timor (Green Guard® against *L. migratoria*, 2004) and Tanzania (Green Muscle® in 2009 against the red locust, *Nomadacris septemfasciata* (Lecoq and Zhang 2019)). In both instances, there was a policy decision to use *M. acridum* due to concerns about contamination based on proximity to water. *M. acridum* was used during the 2019–2021 desert locust outbreak mostly in Somalia. The FAO released tenders for *M. acridum* supply in Kenya and Ethiopia, and samples of the pathogen were sent to Uganda, Pakistan, and India (CABI 2020). Somalia was the only country that decided to use only *M. acridum* and the insect growth regulator teflubenzuron to protect their pastoral system from potentially toxic chemicals. Although there were challenges in conducting field evaluations of the Somali campaign, valuable insights emerged (Owuor and McRae 2022). The effort has been seen as a breakthrough in that it is the largest surface area treated with biopesticides in a single campaign anywhere in the world, with more than 100,000 hectares sprayed with *M. acridum* (CABI n.d.).

The FAO also encourages biopesticide use in Central Asia where there have been trials with Green Guard® (Hunter et al. 2016) and Novacrid® (Latchininsky 2018). Novacrid® (based on the strain EVCH077) is now registered and being tested in Uzbekistan and nearing registration in West Africa with the plan to roll it out soon across the rest of the continent (Lecoq and Zhang 2019). As of 2023, *M. acridum* has also been registered in Kazakhstan.

Advances and challenges.—Mass production, formulation, and application have advanced biopesticide use (Zhang and Lecoq 2021). Recent advances with *Paranosema locustae* demonstrate its utility in locust and grasshopper management with its broad host spectrum of 144 orthopteran species and lack of effect on non-orthopteran insects. However, there is still a need for more research on non-target organisms, as there can be consequences of *P. locustae* use for other Orthoptera (Bardi et al. 2012). Also helpful is its capacity for vertical transmission to offspring through eggs, suitability across ecosystems from tropical to temperate regions, and increased environment and human safety. *P. locustae* has been shown to have a synergistic effect when used in a mixture with *Metarhizium* spp., which potentially weakens the host immune response (Zhang and Lecoq 2021). China's success in producing large quantities of both *P. locustae* and *M. acridum*, as well as a new water-based suspension of *P. locustae*, has helped spur renewed interest from other countries. Another development includes the complete genome assembly and high-quality gene map of *P. locustae*, widening its potential use as a biopesticide worldwide (Chen et al. 2020). In terms of future ideas, China recently isolated a new strain of the fungus *Aspergillus oryzae* (Ahlburg) Cohn from locusts and demonstrated its high pathogenicity to both locust nymphs and adults in the laboratory (Zhang et al. 2015).

Biopesticide challenges: Unfortunately, most locust and grasshopper management programs do not routinely include biopesticides. An assessment of the reasons for low biopesticide use was carried out by the FAO during two meetings. The first occurred in Senegal in 2007, and participants considered the lessons learned from the operational use of *Metarhizium* in Australia, the costs, and benefits of biopesticides, how to develop a supply for operational use, and methods of integrating them into preventative management strategies (Magor 2007). The second meeting happened in Rome in 2009 (FAO 2009, Lecoq 2010), and participants discussed progress in the use of biopesticides operationally, the importance of promoting acceptance, and making further recommendations. Often, there are economic, political, and organizational impediments that limit effective implementation (Gay et al. 2017). For example, many countries use chemical registration procedures for biopesticides, and approval has increasingly high standards. This makes sense for chemical pesticides because of their side effects, such as contributing to insect declines worldwide (Sánchez-Bayo and Wyckhuys 2019). However, this is a potentially overly burdensome hurdle for many biopesticides, which puts them at a significant cost disadvantage as registration costs must be amortized over a single pest type (acridid grasshoppers) versus a broad spectrum of pests as is common with chemical pesticides.

Another major impediment has been the resistance of countries to using foreign isolates for fear of potentially negative impacts on native ecology (e.g., the United States). China and Mexico have found and developed their own isolates from native strains, but other countries have either not been able to find their own or, if they have, they have not been as efficacious as desired. Furthermore, developing local isolates for countries with only occasional outbreaks will likely not be economically viable because of the lack of a regular market. This was the case in Brazil where the low frequency of locust outbreaks meant that the locally developed mycopesticide could not be marketed economically despite its proven effectiveness in the field (Magalhães et al. 2000, Magalhães and Lecoq 2006). Another related challenge is that the mortality caused by biopesticides like *P. locustae* is dose-dependent, meaning that the higher the dose, the higher the mortality. Because it is expensive to rear grasshoppers to produce spores in vivo, the ability to increase spore yield is a barrier to mass production and large-scale application (Zhang and Lecoq 2021).

Other deterrents to the use of biopesticides include the slow rate of mortality following application. Some have tried to overcome this by adding chemicals such as phenylacetonitrile (PAN) (Bal et al. 2014) to the biopesticide or by adding toxins to the *M. acridum* genome (Fang et al. 2014). However, adding chemicals or toxins has meant that these practices have not yet been used in environmentally sensitive areas. Additional challenges include their limited shelf life and a different set of training or supervision requirements for handling, including storing *Metarhizium* spores, mixing spray formulations, and cleaning equipment to ensure the optimal efficacy of biopesticides (Cadmus and ICF 2020). However, despite all these impediments, preventive management programs that have included biopesticides have found them invaluable in being able to treat locusts and grasshoppers wherever they are found. As restrictions on chemical pesticide use justifiably increase, treatment programs must ensure their effectiveness by including biopesticides and putting in place the mechanisms to facilitate their use.

Preventative management challenges.—While enhanced preventive management systems have decreased the duration and scale of agricultural damage and biopesticides offer promising alternatives, there are still significant hurdles to overcome in implementing any preventative practice, chemical or otherwise. Showler (2018), working on the desert locust, identified several interrelated challenges to preventive management that are applicable to other locust and grasshopper species, including:

- Remote, rugged terrain;
- Poor roads and infrastructure, which impede access to breeding areas;
- Political insecurity (e.g., rebellions, banditry, war, and minefields);
- Unpreparedness (which delays detection of breeding populations and population management efforts);
- Environmental concerns (arising from insecticide applications with associated risks to the environment and human safety);
- Research impediments (slow progress toward developing proactive and preventive strategies); and
- Political hindrances and false assumptions around management (as most international aid agency representatives have little or no locust or grasshopper campaign experience).

The discontinuation of projects, loss of organizational continuity, and the disorganization of locust and grasshopper management systems can also occur due to political regime shifts. Examples include African nations gaining independence in the second half of the 20th century during desert locust plagues (Roy 2001) and the collapse of the Soviet Union in Kazakhstan in the early 1990s that hindered response to the 1998–2001 plague of Italian and Asiatic migratory locusts in Kazakhstan (Toleubayev et al. 2007). Additionally, the geopolitical situation and unusually strong tropical cyclones in the Arabian Peninsula complicated desert locust monitoring in 2018, preventing the detection of nymphal marching bands and enabling the development of three generations of desert locusts to go undetected and unmanaged (Lecoq 2021).

Direct political hindrances aside, a major obstacle in locust and grasshopper management is the lack of sustained funding for preventive management. Many authors have decried how funding tracks the cycle of locust outbreaks (Lecoq 1991, Doré and Barbier 2015, Gay et al. 2017). When locust crises abate, research attention and budgets decrease, creating a lag between the problem and new insights. There are also variations in the willingness and ability of impacted countries to take and maintain effective action (Joffe 1995, Lecoq 2001, Symmons 2009). This inconsistency reduces the possibility of developing long-term, effective preventive strategies. This has been demonstrated repeatedly:

- Funding and infrastructure were ramped down prior to the 1987–1988 desert locust outbreak (Lecoq 1991, Roy 2001).
- In 2003, locust control capacities in the West Africa region were deficient, the FAO Emergency Prevention System for Transboundary Animal and Plant Pests and Diseases (EMPRES) program was slow to react due to lack of donor commitment, which had detrimental effects during the 2003–2005 desert locust plague (Lecoq 2005).
- In 2019–2021, previous erosion of monitoring and response infrastructure in the Horn of Africa, due to a long absence of swarms in the region, left them unprepared for the major desert locust plague that occurred (Showler et al. 2021).

Future questions.—Developing new research questions and further integrating biopesticides into management regimes will be aided by the collection and publication of data from recent large-scale uses (e.g., Somalia against the desert locust). Additional testing of the simultaneous use of *Paranosema locustae* and *Metarhizium* spp. for high-density locust and grasshopper outbreaks is needed as well as creating new formulations and technologies to improve the efficiency of spore production and maintain high spore viability. Further understanding of the molecular mechanisms and interactions of these biocontrol agents is needed to improve traditional in vivo production or to find alternatives. Continuing the development of genomic and transcriptomic resources for both proven biopesticides and candidate organisms will be a foundational resource for enhancing biopesticide efficacy and finding solutions to some of the current challenges in their wide-scale implementation.

Transdisciplinary opportunities.—Solving the challenges to successful preventative management and biopesticide use hinges on the ability to collaborate, share information, and work across disciplines. The successful coordination of a campaign often involves scientists working with government officials and decision-makers, farmers working with locust and grasshopper officers, and stakeholder groups/non-profits/NGOs working with various parts of these systems. Biology research could provide better insights into how ecological factors affect treatments as well as the mechanisms underpinning these interactions. Social science could play an important role in understanding what drives human decision-making during management programs and where organization and preparedness break down.

Key reviews and synthesis articles.—Cullen et al. (2017), Zhang and Lecoq (2021), Zhang et al. (2019)

Social sciences

By Clara Therville, Joleen Hadrich, Michel Lecoq, Jeffrey A. Lockwood, Cyril Piou, Brian E. Robinson, Mira Word Ries

Background.—The social sciences include a wide range of disciplines that study human behavior and its societal and cultural dimensions. Even though locust management and research are part of a complex SETS, the majority of research has focused on natural science without including the complexities of the social dimension. We now fully recognize the coupled social-ecological systems that make these issues complex (Cease et al. 2015) and understand that the sustainability of locust management systems is severely constrained by social, economic, organizational, and cultural factors (Therville et al. 2021). According to Lecoq (2005, 2021), ecological research "... is no longer the key limiting factor with respect to plague control." Many authors are calling for a more robust inclusion of social sciences into the study of locusts (e.g., Lecoq 2001, 2005, Lockwood et al. 2001, Showler 2003, Belayneh 2005, van Huis et al. 2007, Symmons 2009, Zhang et al. 2019, Meynard et al. 2020, Lockwood and Sardo 2021, Showler et al. 2021, Therville et al. 2021), especially regarding stakeholders' strategies and governance issues, but also to invent new ways of interacting and living with locusts (Cease et al. 2015, Lockwood and Sardo 2021, Therville et al. 2021).

The social sciences have contributed to our understanding of locust management as well as locust impacts. Methods and perspectives for understanding the interactions between locust plagues and societal vulnerabilities or recovering capacities are increasingly important in the face of interconnected hazards. While socio-economic studies have been conducted to assess the consequences of locust plagues on livelihoods (e.g., Crook et al. 2020), many of these focus on measuring the impacts of outbreaks by considering the cost of control operations and the amount of crop damage averted (U.S. Congress 1990, Joffe 1998). Reported statistics on the amounts of crops saved through control campaigns often give a simplified portrayal of success and omit the cascading effects of other socio-economic issues such as displacement, resource competition, or the aftermath of pesticide use from an environmental and human health perspective. We also ought to recognize the incommensurable values (e.g., the price of food, the importance of traditions and culture, the cost of physical and mental human suffering, and the enduring deleterious effects on the environment, child development, and educational outcomes (De Vreyer et al. 2015)) that cannot be readily reduced to common units for quantitative analyses. Additionally, it is necessary to acknowledge that, for many stakeholders, locust management is only a portion of a portfolio of risks that they must manage. Short-term concerns focused on one acute risk may exacerbate the risk of locust outbreaks in the long term, and human behavior can only be well understood in context.

As Therville et al. (2021) detail, social science could help uncover a deeper understanding of the institution of locust management and research, especially the paradox of building long-term collective action in the face of a double uncertainty, the first being temporal, as long periods between outbreaks can lead to the loss of expertise and capacity or even belief that an outbreak will likely occur, and second being spatial, as outbreak locations and invasion areas can be uncertain, as can social capital. Recent studies on locust management from a social sciences perspective highlight the responses implemented by locust managers to face these challenges and the associated fragilities (Therville et al. 2021, Korinth 2022). For example, if prevention is successful, a major reduction of locust outbreaks may amplify the "oblivion phase" in the vicious cycle of locust management during which there is a lack of motivation and the issue has been forgotten, thus making management when an outbreak returns more challenging and, once again, triggering a crisis. In such a context, focusing on maintaining operations, strategies, and collaborations during recession times (e.g., through simulation exercises or archiving knowledge and experience for future locust field officers and operations managers) is key (Gay et al. 2021).

Advances and challenges.—Perhaps the most fundamental contributions by the social sciences regarding locust management have been made by illuminating issues and problems with weak actionable progress and results regarding control campaigns (Therville et al. 2021, Korinth 2022). Quantitative research on locust management does not always translate into better or more effective monitoring and management due to at least two central issues. First, locust management is fundamentally a collective action problem (since neither a farmer nor a country can manage the problem alone due to migration and impacts that 'spillover' into other's property). Second, addressing collective action is challenging due to the risk of free riding. Pragmatic management of locusts is also hindered by 1) the scale of the problem and spatial uncertainty, leading to difficulty implementing trust, shared vision, and coordinated action and 2) either low frequency but consistent patterns of damage or large-scale but infrequent patterns of damage, both of which inhibit investing in an effective preventive system through time. What is the gain in investing in something when you are not sure the problem will arise or even if the problem exists? Managing landscapes for better social control of locusts in a way that benefits everyone can sometimes come at a cost to individual farmers.

Management strategies can also be hindered because scientists studying locusts are often geographically distant from wild locust populations. This can make it challenging to understand key contextual factors that might affect locusts, management actions, or how these vary across time or space. Further complicating things, there can be a disconnect between the interests of scientists, farmers, and other stakeholders, sometimes even a contentious divide between the management strategies of plant protection agencies and local customs, beliefs, and values (Gagné 2022).

Qualitative research that considers the human dimensions of locust management issues may help bridge some divides in places where this tension is felt. For example, in the event of an outbreak, some farmers wish to have plant protection agencies come immediately and repeatedly to spray pesticides (unpublished interviews 2017 within Word et al. 2019). Others prefer no chemical treatment, and others resist interventions altogether because of religious beliefs, as was the case for some people living in Zanskar, a remote region of the Himalayas, during a 2016 locust invasion (Gagné 2022). This research investigated how locusts emerged in Zanskar as a politically and morally charged creature by challenging religious beliefs that stress non-violence and cohabitation with nonhuman others in the face of crop loss. The researcher observed the actions people took to avoid harming any insects, such as avoiding driving during a locust swarm or pouring out pesticides, despite the impacts on their livelihoods. This type of fieldwork is essential to widen the diversity of perspectives around how people interact with locusts and why and helps demonstrate that one size does not fit all and that a 'spray and suppress' approach to management is not the only way. Some communities may prefer to learn, or teach, alternative methods that operate outside of the lens that views locusts as pests and instead turn them into income, food, fodder, fertilizer, or even develop non-destructive methods of insurance and safety nets that emerge to cope with the periodic presence of locusts.

With recent studies linking land management decisions and locust population dynamics (reviewed in Le Gall et al. 2019, Word et al. 2019), there is progress in integrating the SETS framework into field ecology experiments. Economists have also explored the balance between managing ecosystems for agricultural production *vs* other ecosystem services, including managing locust populations. For example, Byrne et al. (2020) used 'payments for ecosystems services' methods to estimate a fair subsidy level that would compensate herders in Inner Mongolia, China, who reduce grazing to sustainable levels and thus help prevent locust outbreaks. These herders face a difficult tradeoff: land is degraded when they overgraze, but they lose profits when herds are smaller. Furthermore, when land tenure security is low, many herders overgraze since their longer-term access to the land is uncertain (Robinson et al. 2018). One solution is for governments to run compensation policies that subsidize herders. Models based on the Senegalese context explore how livestock insurance dynamics under a variety of potential economic institutions influence outbreak risk (Berry et al. 2019). Perfectly compensating at-risk herders fails to correct the underlying externality. In Inner Mongolia, such payments have been paid but likely need to be more closely enforced to affect herder behavior (Byrne et al. 2020). While herders may increase short-term profit by overgrazing, they may unknowingly be developing an environment favorable for locust outbreaks, creating future negative financial impacts. The spatiotemporal scale and integration of many stakeholders mean that humanities scholars and social scientists, along with natural scientists, have the opportunity to promote participatory work that helps find viable land management options that balance these tradeoffs (Cease et al. 2015).

Future questions.—Social science is underdeveloped in locust research, and multiple questions remain poorly addressed, especially those intended to understand the social–ecological context, the human dimensions of control campaigns, and the social impacts of locust outbreaks. Social science can be applied to decipher if and how collaboration is effective and at what scale (Therville et al. 2021). Future research paths for social scientists could focus on how to identify organizational weaknesses before they reveal themselves in a crisis (Therville et al. 2021), increase engagement with farming communities, and, above all, question dominant paradigms in order to challenge power dynamics and the status quo to bring new and more sustainable approaches to locust management. Political ecology is a field that may provide insights into navigating the power dynamics that pervade any management context, especially those that are present in resource-based contexts. Finally, co-producing research with communities while integrating local or traditional knowledge approaches to manage complex problems is showing great promise in devising locally applicable and sustainable solutions. Better engaging communities to help define research questions and potentially participate in research activities will help improve the feasibility of management actions and solutions.

Transdisciplinary opportunities.—In addition to calling for more collaboration between natural and social scientists, we encourage the involvement of social science disciplines that are less represented in locust research, such as communications, sociology, religious studies, anthropology, and psychology. Transdisciplinary studies of other complex social–ecological systems may also offer insights and feedback for practitioners, natural scientists, government officials, and other decision-makers.

Key reviews and synthesis articles.—Lecoq M (2005), Therville et al. (2021), Lockwood et al. (2001)

The humanities and ethics of locust control

By Jeffrey A. Lockwood, Mira Word Ries, Ted Deveson

Background.—The arts and humanities are important to transdisciplinary approaches to environmental management issues including locust and grasshopper outbreaks because they present different perspectives on problems that have been seen largely as scientific and technical. They can also connect with individuals representing components of societal groups that were previously uninitiated and unengaged in the problem. This, in turn, can provide ideas that could lead to novel, inclusive, ethical, and morally defensible solutions. Contributing disciplines include histories from local to transnational; the history and philosophy of science; science and technology studies; philosophy; the environmental humanities with its associated fields of environmental history, ecocriticism, and other modes of expression; along with literature, poetry, and the performing and visual arts.

Environmental humanities seek to understand what it means to be human as a causal and moral agent in an ecological context (Sörlin 2012, Palsson et al. 2013) and emphasize the fundamental questions of value, responsibility, and purpose in a time of rapidly accelerating change (Rose et al. 2012). They offer the potential for methodological and conceptual innovation at the interface of environmental and social problems through collaborations with scientific and engineering disciplines. Locust work could therefore benefit from a stronger inclusion of history, literature, religious studies, and philosophy.

Histories.—Agriculture and locusts have deeply linked histories. The entanglement of agriculturalists with locusts being unpredictable, destructive antagonists stretches back to the first agricultural societies, although other positive perspectives that link locusts to food and culture certainly exist (Kamienkowski 2022).

Our understanding of the ecology, infestation patterns, and distribution of numerous locust species draws upon a long history of observing their occurrence, behavior, and environmental conditions. Along with the variety of human responses, these early observations form part of the environmental histories of human–locust interactions. Through these histories, the association between changes in locust outbreaks and land use and land cover changes, both human- and climate-induced, has frequently become apparent. The realization of that link, however, is not new. In the 1950s, Boris Uvarov recognized that this had long been known by his decision to use the Arabic name 'djerad el adami' (man's locust) for the Moroccan locust (Uvarov 1956).

This history of observing and recording locust outbreaks has produced detailed historical databases of occurrence for numerous species. These are a record of geographical locations of locust distribution over time, along with estimates of population and spatial scale fundamental to characterizing their outbreaks. The longest recorded sequences come from the unique continuity of Chinese court agricultural documents that stretch back more than a thousand years (Tian et al. 2011). In the 20th century, yearly, seasonal, and even monthly datasets covering many decades were collated from reports, surveillance, and agricultural extension programs for species in Africa, Asia, North and South America, and Australia. Typical early examples of data explication were time-series bar graphs of the number of districts affected (e.g., Gastón 1952, Waloff 1976, Wright 1987). The methodology of gridding desert locust records across Africa and western Asia, developed by the Cartographic Unit of the Anti-Locust Research Centre (ALRC), headed by Zena Waloff in the 1950s, provided the basis for analyzing migrations and forecasting population dynamics and was subsequently adopted in other countries.

These accumulating historical datasets, now collected to the moment and meter rather than province and year, have in this century become source data for analyses against other time-series environmental data to characterize potential and causal ecological relationships and help predict near-term changes (Stige et al.

2007, Tratalos et al. 2010) or possible dynamics under long-term future climate change scenarios (Wang et al. 2019, Meynard et al. 2017). Increasingly, sophisticated statistical tests and algorithms, such as wavelet analysis and machine-learning estimates of fit, are being applied to these historical data, although the results and interpretations may differ (Yu et al. 2009, Zhang et al. 2009b).

Locust migrations propagated the risk of crop damage over large geographic areas and across borders, resulting in the involvement of states in organizing collective actions, scientific investigations, and creating laws and institutions to control the pests. These endeavors were enmeshed with parallel histories of technology, instruments, field methods, and insecticide chemistry. Agricultural and economic history is also relevant to incorporating broader ecological and social frameworks into sustainable responses. The capacity to manage plagues is specific to the ecology of each species but also to the environmental history, landscape ecology, and political geography of the people and areas affected. The 1880s–1960s saw repeated, intense locust plagues on several continents, particularly in Africa where imperial European powers directed scientific resources in efforts to alleviate famines but also to maintain their techno-political soft power (Péloquin 2013). The sequence of responses to these plagues produced numerous cooperative institutions for research, monitoring, and control, with continuity to some present transnational institutional arrangements.

Institutional involvement in locust problems has also evolved over time, with opportunities for matching governance structures and funding to the scale and frequency of outbreaks. The reasons for and how institutions were created are also relevant to their effectiveness and ability to adapt (Dovers 2000). An examination of the history of locust management offers insights for future public policy decisions. The history of past practices can also shed light on social-ecological traps (Boonstra and de Boer 2014), such as cycles of overgrazing or climatic shifts common to many locust-affected communities, and on appropriate scales and capabilities to aid applied science solutions involving community-based management programs (Word et al. 2019, Le Gall 2020b). Similarly, local histories of people affected can identify perceptions of the problem and the scale of the sustainability threat (Gagné 2022, Kamienkowski 2022). Previous policy failures may have resulted from inappropriate science and engineering information or from top-down bureaucratic management that can stifle local expertise, engagement, and adaptive responses. In the heat of major plagues, there has been little choice but to apply one-size-fits-all strategies and technologies, but preventive local actions, including land-use decisions, could reduce the incidence of plagues.

The imperative to reduce populations during plagues tied institutions to insecticide science and delivery systems. Before the 20th century, public collective manual controls were mandated or encouraged by almost all administrations, but after each World War, locust control followed the sequence of insecticides roughly linked to chemical warfare research: arsenic, organochlorine, and then organophosphate compounds, coupled with aircraft spray technologies (Russell 2001). Insecticides from these synthetic organic chemistry groups were each found to have negative effects on human health and the environment as well as resulting in insect resistance, albeit not clearly among locusts, and many were gradually withdrawn from agricultural applications. Different chemistries have since been used for locust control, but like the previous synthetic insecticides, unforeseen negative consequences have emerged in some cases (Peveling 2022). The widespread use of insecticides in agriculture and locust control has created geographical and social inequalities in exposure risks.

The published history of scientific locust research now spans three centuries. Not only does it trace the many significant contributions to applied and fundamental entomological science, it also exposes the motivations and paradigms of its practitioners over several human generations. The history of science has shown that individuals involved in this collective and cumulative enterprise are also influenced by contemporary ideas circulating within their institutions and across the wider society. This might be cause for some self-reflection by scientists about their own precepts.

Art.—Art has informed our perceptions of locusts for millennia, ranging from paintings of locusts on Egyptian tombs in the 11th century BC to cartoons by 19th century U.S. illustrator Henry Worrall, from the surrealist paintings of Salvador Dali to modern musical performances (Milius 2018, Lockwood et al. 2020). Many entomologists were also artists, and their detailed work has contributed to our understanding and perceptions of the insect world. From the 19th century come the names of such prominent taxonomic illustrators and engravers as Donovan, Curtis, and Westwood, while in this century, the many Orthoptera illustrated and described by Daniel Otte show the continuity of that artistic tradition. Locusts are present in Indigenous traditions (e.g., Kamienkowski 2022), the Bible, the Quran, the Sanskrit epic poem "Mahabharata," and the equally ancient Iranian Zoroastrian Vendidad (Cressman and Elliott 2014). Even further back, the first known representation of an insect was engraved on a bison bone found in the Trois-Frères cave in France and dating from the Middle Magdalenian period (14,000–13,000 BC) (Chopard 1928, *Catherine Schwab, pers. commun. 2017). This ancient artifact dates from before agriculture was developed and apparently represents a grasshopper whose outbreaks could offer food resources to local human populations (*Laurent Pelozuelo, pers. comm. 2017) or perhaps devastate natural yields. In popular culture, insects or locusts have been featured in movies, representing such narrative tropes as nature's revenge, metamorphoses, or the mutant-horror of unwanted others. Nature documentaries also regularly include dramatic scenes of myriad locusts on the move. Hence, our dynamic, complex, and competitive ecological relationships with locusts have often been expressed through story and art. To analyze our current conceptual framework and then reshape this structure to better reflect contemporary science, it is important to understand the cultural roots of modern paradigms.

Advances and challenges.—The long, competitive, and changing relationships between humans and each locust species are epitomes of environmental history, and the insects themselves are powerfully familiar historical agents (Deveson and Martinez 2017): locust populations responding to environmental events directly influenced the course of public science and, through it, ecological science, as major plagues often produced pulses of government-directed research.

In the 20th century, human–locust relationships inevitably intersected with the politics of pesticides. The related institutional decision-making and consequences for the geography of public health were unavoidable in the context of modern humans' most fundamental environmental activity—agriculture. In *War and Nature*, Edmund Russell described how after both World Wars, there was a deliberate diversion of military chemists and their products to a new war with insects as the enemy and observed that 'the triviality of insects removed the stigma of poison gas, and the technical achievements of war elevated the significance of entomological pest control' (Russell 2001). Learning of the negative consequences that the 'war' against insects had on people and nature in the United States triggered Rachel Carson's 1962 seminal environmental history *Silent Spring* (Carson 1962), which led to a wider environmental awakening.

It took longer for that awakening to be applied in many locust-affected countries, but the recent development and increasing success of biopesticides, particularly mycopesticides, is bringing a fundamental change to the problematic century-old paradigm of locust control (Lecoq and Cease 2022b, Owuor and McRae 2022). The progress provides for a growing level of environmental justice to millions of vulnerable people who are subject to the geographical inequalities of insecticide exposure: not only those whose bodies or food sources might be subject to direct spraying or pesticide drift but also those engaged in the repeated handling, transport, mixing, and spraying of insecticides. It also offers more defensibility to difficult decisions involved in organizing major control operations. Coupled with precision spray technologies and data logging, progress should include greater accountability for the deposition of all insecticides. However, even biopesticides come with a risk of unforeseen consequences, particularly for other insects and orthopterans (Bardi et al. 2012).

Scholars, managers, and policymakers have begun to understand that substantive progress in locust management must extend beyond fiscal considerations. The inclusion of natural processes and non-human species in assessing the value of a pest management practice represents a substantial advance (e.g., preservation of endangered species, protection of pollinators, conservation of wildlife habitats, and safeguarding of clean water).

However, further progress toward transdisciplinarity should include marginalized people. A locust management program based solely on environmental or financial considerations might well be justified in letting some people starve or be driven from marginally productive land if the ecological or monetary costs of avoiding such outcomes exceed the benefits. Indeed, there is no assurance that a socioeconomically or even ecologically sustainable practice will not treat people as expendable or their suffering as defensible—outcomes that we can readily recognize, and learn from, in human history.

Future questions.—Researchers must explicitly recognize the is/ought distinction: just because a practice is used or can be developed to manage locusts does not mean it is an action we ought to take in an ethical or a religious sense. How to include axiology (the study of values) in deepening and expanding our understanding of locust management is a vital question in the coming years.

Philosophy—ethics in particular—plays a vital role in locust research and management (Lockwood and Sardo 2021). We can understand our moral obligations via utilitarianism (that which produces the greatest good for the greatest number), deontology (that which aligns with our duties to respect the rights of others), or virtues (that which makes for human flourishing and the realization of our potential). While these frameworks give rise to important questions (e.g., what is the "greatest good" in locust management, and what are our obligations to future generations in locust-affected countries?), philosophers such as Lockwood and Sardo (2021) note that issues of justice require constructs other than—or in addition to—those moral agents. Justice entails collective responsibilities that cannot be reduced entirely to individual obligations (Rawls 1999, Nagel 2005).

To strive for international justice, we must begin by answering two questions: 1) Who is morally responsible for addressing acute humanitarian crises during locust plagues and for developing ongoing systems to prevent future disasters? Potential agents include individuals, intergovernmental agencies, nation-states (both those afflicted and assisting), government agencies, non-profits, scientific consortia, and private corporations. But which of these have moral duties—and why (Erskine 2001, O'Neil 2001)? 2) How should we distribute responsibilities among agents during and between outbreaks? The principles of justice adapted by Lockwood and Sardo (2021) from Miller (2001) to construct their analytical framework include causal responsibility (who contributed to the harm?), moral responsibility (who can be blamed for the harm?), capacity (who can remediate the harm?), and community (who has relationships entailing obligations to remediate the harm?). Thus, while the social sciences provide a descriptive account of the agents and their proportionate responsibilities, philosophy addresses the normative concerns: what we ought to do about locust management.

Transdisciplinary opportunities.—The greatest obstacles to pest management may be a lack of public knowledge and political will. The potential of the arts to convey scientific knowledge has been explored using virtually every genre (Lesen et al. 2016, American Academy of Arts & Sciences 2017). However, as much as artistic expression might be an effective means of communicating science, it is important to also recognize that art is not merely a way of making science digestible (Dressler and Borrelli 2018). Art should be a full partner with science in efforts to understand the natural world through the capacity of the artist to perceive locusts in ways that challenge, stimulate, and startle researchers. Art is also a powerful way to understand how emotions are involved in our capacity to face environmental problems such as locusts.

A bridge from the humanities to science and management is found in the metaphorical structures (Lakoff and Johnson 2003) that shape how we think of locusts and our relationship to them. A metaphor is a way of understanding the unfamiliar (locusts) in terms of the familiar (humans). For example, since the First World War, military metaphors have dominated locust control terms, including outbreaks, campaigns, invasions, and targets, reflecting locusts as enemies invading our territories. We can even frame control programs in terms of Just War Theory (Lockwood 2005). For example, as in war, a reactive locust control program can be critiqued as being a last resort, being declared by a proper authority, possessing the right intentions, having a reasonable chance of success, and having the ends proportional to the means used. But is war the best metaphor applied to locust management? The humanities have the capacity to challenge the conceptual status quo and cultivate alternative frameworks. Instead of framing locusts as an enemy to be eradicated, managers could be mindful of their cultural history, environmental role, and position as living creatures capable of being harmed. Collaboration with artists, psychologists, and social scientists could help understand and, therefore, help shape alternative management decisions. The way locusts will be viewed in the future may also be radically different depending on the responses of different species to environmental changes and human perceptions and utilization of insect resources.

Key reviews and synthesis articles.—Carson RL (1962), Lockwood and Sardo (2021), Miller (2008), Russell EM (2001), Sörlin (2012)

Conclusions

The road ahead

Although not all species and regions affected by locust and grasshopper outbreaks could be covered in this paper, we hope to have shown how locust management and research need to be addressed as a complex adaptive system with sustained global attention and resources. Working in transdisciplinary teams connects the related, but often isolated, spheres of locust research and management, particularly between laboratory-based researchers and stakeholders working with locusts in the field. Integrating disciplinary teams creates the foundations for inclusive perspectives that are more useful for decision-makers and applicable under evolving scenarios that consider global change.

Many organizations recognize that locust management requires ongoing preventive management, but there are still large fluctuations in funding and focus. Such fluctuations are likely the foremost challenge for the farmers, land managers, and scientists whose livelihoods depend on understanding locust and grasshopper populations. During locust or pest grasshopper outbreaks, governments, companies, and NGOs dedicate large amounts of resources to locust monitoring and control. However, a serious constraint to swift control campaigns is often the delay in releasing and allocating funds required by national teams to match the speed of outbreak developments (van Huis et al. 2007). Even with substantial organizational involvement, the struggle to maintain funding, personnel, and relevance during times of low locust and grasshopper activity remains a challenge. Convincing donors, governments, and other funding sources that resources are well spent in times of locust recession remains difficult, even though research has shown the financial benefits of this approach (Gay et al. 2017). However, consistent progress during recession times is critical. Effective and environmentally conscious management that reduces impacts on livelihoods depends on the combination of well-established operating procedures as well as the accessibility of sustainable approaches and a willingness to innovate. There are numerous and growing ways to direct resources that will increase our global capacity to control pests, even in non-outbreak years.

Examples include the following:

1. Advancing biological, ecological, and social science research.
2. Improving and implementing existing technologies.
3. Testing the readiness of the various actors involved in locust and grasshopper management, the various communication channels, and the response times in emergency simulation exercises.
4. Standardizing protocols and emergency action plans.
5. Developing and testing biocontrol options and methods.
6. Conducting environmental impact assessments.
7. Creating prevention plans.
8. Mapping environmentally sensitive areas and identifying where human health risks are high.
9. Increasing local educational outreach and capacity building.
10. Maintaining and enhancing a global network for information sharing.
11. Cross-training technicians/managers across services/training reserve teams.
12. Preparing for relations with the media and various national and international actors in the emergency period as well as in times of remission so that everyone knows that the prevention mechanism is operational.
13. Creating a global network promoting expert/technician/student exchanges; if something is happening in one part of the world, people could be sent there to keep their skills up to date.

Achieving and maintaining cross-organizational collaborations is a challenge because it requires trust and a consistent stream of funding for travel, training, and resource sharing. Most locust research happens in laboratories in the Global North, but most locusts outbreak in the Global South. Thus, the scientists studying locusts and the wild populations of locusts are often geographically distant from each other, and researchers in countries with substantial science funding are challenged to convince their country to support consistent funding for a pest that does not present a direct threat. It is particularly important to recognize that most researchers depend on collaboration with local management organizations that possess essential staff, equipment, logistical expertise, and an intimate understanding of locust ecology and field conditions. Without the support of such organizations, conducting meaningful locust research becomes an immense challenge. Integration happens when local experts are true collaborators and co-creators acknowledged for their work and are involved with the research and publication writing. These collaborations best support research advancements that are meaningful for, and can be best integrated into, locust management. Translating basic locust research into effective monitoring and control requires interactive feedback and collaboration between scientists, locust control teams, and affected communities. However, barriers, such as obtaining travel visas, can be long, burdensome, and expensive, making it difficult for stakeholders to work together. Recognizing these logistical barriers and creating programs and pathways to specifically support large-scale collaborations and including more diverse perspectives will bring important insights that are context and culturally specific.

Another concern is the need to raise environmental and public health standards in locust control, which can help to maintain resources and find donors. The reduction of impacts on the environment and on human health must be strategic: guidelines should be followed to carry out large-scale operations whether they use chemical pesticides or biocontrol, with a minimum impact. Tools such as standardized environmental impact assessments that rely on robust scientific data are essential to demonstrate the effect of efforts made to limit the social and environmental consequences of locust control. In addition, developing a socio-economic argument focused on avoiding long-term costs, negative human health outcomes, and other externalities could enhance international cooperation.

New technologies raise research and management questions on a global scale. Technology using drones, small cameras, or remote sensing can address new research questions about locust bioecology and can change monitoring and control practices. However, these technologies face two possible risks: declining interest in fieldwork and the need for the financial resources required for development, especially during non-plague times.

Many soft skills are also required to maintain the important professional and political relationships that facilitate integral services in a well-functioning organization. Intangible qualities such as trust, cooperation, and collective learning are equally important to locust control, along with the capacity to face social barriers, such as conflicting interests and perspectives within communities, loss of knowledge when employees retire, reluctance to change, language and cultural differences, or shifting political priorities to respond to public demand.

Role of the Global Locust Initiative (GLI)

Arizona State University launched the GLI in 2018 as a response to some of these challenges. The initiative welcomes individuals with interests in locusts and grasshoppers, transboundary pests, integrated pest management, landscape-level processes, food security, and/or cross-sectoral initiatives. GLI has two arms: (1) the GLI Network, which links stakeholders and experts from around the world to share ideas and forge collaborations, often through workshops and networking events with the goal of facilitating research and developing sustainable solutions for the global challenge of locust and grasshopper management, and (2) the GLI Laboratory, which hosts ongoing projects ranging from locust physiology and ecology to community-based pest management and locust governance.

All discussion groups at the 2018 launch conference mentioned the usefulness of workshops, training, and collaborative educational forums (online or in-person). With the capacity to join meetings, workshops, and conferences online, we have even more opportunities to collaborate and share information. Areas where we need to bring a variety of stakeholders to the table to create synergies and make advancements include the following:

1) Connecting molecular biology to whole organism phenotypes, populations, and ecosystems—launched by the newly created Behavioral Plasticity Research Institute (BPRI), including training in the appropriate storage and collection of field samples for later molecular analysis (e.g., Chapuis et al. 2008, 2011, Ma et al. 2012).
2) Ecological modeling to enable researchers to integrate datasets of locust occurrence and movement patterns across the globe, including using geographic information system (GIS) analyses of satellite and other landscape-scale data sets (Latchininsky and Sivanpillai 2010, Latchininsky et al. 2016).
3) The use of drones to measure and analyze locust movement on a smaller scale (see Section 8 in Cullen et al. 2017).
4) Experimental design and ways to collect data that are suitable for wider dissemination and analysis.
5) Locust husbandry and rearing to establish colonies of a wider range of locust species worldwide with fewer genetic bottlenecks (Berthier et al. 2010, Cullen et al. 2017).
6) The management and curation of large datasets to create coherent and integrated data resources for all stakeholders.
7) Understanding the complex responses of locusts and locust-affected regions to climate change.

Sessions on cross-sectoral collaboration and networking would be beneficial to ensure that all stakeholders are fully connected and aware of the challenges that colleagues face. To this end, the GLI established a collaborative online community called "Hopperlink" to ensure that all stakeholders have an opportunity to connect directly and share experiences, resources, and events. There is also a new project called HopperWiki that strives to be a global archive and information hub for all things related to locusts and grasshoppers. To contribute or learn more, visit www.HopperWiki.org. Other desired initiatives include developing strong exchange networks and training opportunities for students with a particular focus on exchanges between countries, studying the impacts of climate change, developing methods to estimate density and numbers of locusts, models, and scenario building, or conducting research on how organizations interact and connect. In many ways, it is unrealistic and unnecessary to have high-level infrastructure persist all around the world. Rather, in areas outside permanent breeding zones, we should create more global resources that can be mobilized quickly. Visit the GLI website to join the network www.locust.asu.edu and connect to many of the organizations and individuals mentioned in this article.

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Supplementary material 1

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Explanation note: Locust and grasshopper organizations.

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Supplementary material 2

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