A Review of the Biology, Ecology, and Management of the South American Locust, *Schistocerca cancellata* (Serville, 1838), and Future Prospects

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Abstract: In the first half of the twentieth century, the South American Locust (SAL), *Schistocerca cancellata* (Serville, 1838), was a major pest of agriculture in Argentina, Bolivia, Paraguay, Uruguay, and Brazil. From 1954–2014, a preventive management program appeared to limit SAL populations, with only small- to moderate-scale treatments required, limited to outbreak areas in northwest Argentina. However, the lack of major locust outbreaks led to a gradual reduction in resources, and in 2015, the sudden appearance of swarms marked the beginning of a substantial upsurge, with many swarms reported initially in Argentina in 2015, followed by expansion into neighboring countries over the next few years. The upsurge required a rapid allocation of resources for management of SAL and a detailed examination of the improvements needed for the successful management of this species. This paper provides a review of SAL biology, management history, and perspectives on navigating a plague period after a 60-year recession.

Keywords: locust plagues; population dynamics; management

1. Introduction

Locusts are among the most devastating pests globally and leave clear imprints in memories and historical records. The substantial impact of the South American Locust (SAL), *Schistocerca cancellata* (Serville, 1838), on agriculture and cattle production shaped the early stages of the government agricultural service in Argentina. Going back at least to the first half of the nineteenth century and during the first half of the twentieth century, there were frequent plague periods where SAL invaded other countries, including Bolivia,

Paraguay, Uruguay, and Brazil [1]. The available historic records show that recession periods were the exception rather than the rule [1], but between 1954 and 2014, coinciding with the implementation of a preventive management program, there were no large-scale upsurges, with only localized outbreaks from time to time within Argentina [2,3]. However, there was an upsurge in the number of swarms in Argentina in 2015, and by early 2017, swarms reached Bolivia and Paraguay [3]. This rapid expansion of the locust populations meant that the infrastructure for managing locusts had to be quickly rebuilt.

Locusts differ from most agricultural pests. They are sporadic, have the capacity to rapidly expand across borders, and then contract to localized pockets that act as reservoirs for future outbreaks [4]. The key to successful management is not only knowledge of locust biology and design of sound management strategies but also a robust organization and maintenance of stakeholder engagement. In the case of SAL, a preventive strategy was established by the Argentinean government during the mid-1950s. Organizations for permanent surveillance and control of locusts were established as part of Departments of Plant Health and Acridology of a number of provinces in northwest Argentina [1]. The preventive management system successfully kept SAL populations quite low and generally limited to Catamarca and La Rioja, where preventive management actions were systematically conducted by field teams. The preventive management went largely unnoticed so that the general public thought that the pest had been eradicated, and with no obvious outbreaks, political support and funding gradually declined [2,3]. Thus, the recent resurgence of SAL, six decades after the last major plague, meant public agencies as well as private stakeholders faced the challenge of recovering capacities to deal with an almost forgotten problem.

Across six decades, many things changed, with the most relevant and apparent being land use and the emergence of a more complex matrix of stakeholders. Additionally, there was a change in the way complex problems were dealt with, with a clear worldwide claim for and trend of more participatory approaches for diagnosis, research, and innovation. Naturally, the key questions are (1) "why" and "how" did SAL re-emergence happen, and (2) how to best manage the system into the future. The answer to the first is likely a complex combination of factors including changes in the natural system (land use and convergence of favorable meteorological conditions likely attributable to climate change), and a reduction in monitoring and control operations. To begin to answer these questions, we need to revisit what we know about the problem from different perspectives, considering the new context in terms of the scientific, technological, agricultural, and social matrix.

The present article reviews SAL biology, including a description of typical habitats, temporal changes, and migration, as well as how management changed during the twentieth century. With the sudden and unexpected resurgence of SAL in 2015 [3], a whole new process began, characterized by a steep learning curve in the face of a dramatic upsurge in locust numbers. This process involved the engagement of new stakeholders and cooperation on different fronts that had not been experienced previously: research and development, governance of the emergency, and management of the pest. The review also identifies old and new knowledge gaps, highlighting research and development needs, and thus provides a contribution to redesigning a robust management strategy.

2. Biology and Ecology of *S. cancellata*

Locusts are grasshoppers in the family Acrididae that have a phenotypic plasticity known as phase polyphenism in that they behave as solitarious individuals at low densities but shift to a completely different behavior and morphology when at high density [5]. At low density, locusts are *solitarious:* they avoid each other and are generally cryptic green or brown. Crowded locusts are *gregarious:* they tend to have darker or aposematic coloration and their attraction to each other leads to marching bands of nymphs and migrating swarms of adults. The genus *Schistocerca* (Acrididae, Cyrtacanthacridinae) includes about 50 species, and at least four are considered highly swarming locusts: the desert locust (*S. gregaria*); the Central American locust (*S. piceifrons*); *S. interrita*, which had several major outbreaks in

Perú; and the South American Locust (*S. cancellata*) [6]. *Schistocerca cancellata* is similar to the three others in coloration and body size and can be differentiated by the male cercus, with the lower lobe larger than the upper lobe; by the subgenital plate of males with a notch almost parallel sides; and by the presence of a waxy secretion on the abdomen on mature adults [7,8].

2.1. Phenotypic Plasticity Traits in S. cancellata

2.1.1. Nymphs

Morphology. In the laboratory, the nymphal body size is affected by rearing density, and there is a sex-dependent pattern. Crowded final instar female nymphs are smaller than those reared isolated, while crowded male nymphs are larger, resulting in a less pronounced body size difference between crowded males and females [9] (Table 1). In the field, sexual dimorphism has not been thoroughly studied, though recent observations in Argentina (Piou et al., unpublished data) suggest that female nymphs are larger than males. In both sexes, isolated nymphs have higher density hair on the outer surface of the hind femur, suggesting that this species might use the same mechanism as the desert locust (stimulation of these hairs from bumping into other locusts [10] to detect changes in density) [9].

Coloration. Solitarious nymphs are generally green, with variations from light brown to light green, and small black dots over part or all of the body (e.g., hind femur) (Table 1, Figure 1). At high density, gregarious nymphs exhibit the contrasting pattern of striking yellow, red, or reddish orange and black though some bright yellow nymphs are seen [9] (Figure 1). Between the two extreme colorations typical of the solitarious and gregarious phases, transitional colorations are commonly observed, corresponding to the "transiens" phase [9]. In the laboratory, recently hatched nymphs are generally light green with or without darker areas, and with nymphs kept in isolation, the greenish or light brown coloration is maintained [9]. With nymphs kept at high density, the black pattern is evident within a few hours of hatching. The first two instars are rather pale with the orange-red color of the head and the bright black and yellow becoming more evident after the third instar. However, nymphs crowded for several hours and then isolated initially developed coloration typical of crowding but lost their coloration after the first molt.

Behavior. In its natural habitat, after hatching, solitarious SAL nymphs disperse in the vegetation and develop in isolation, hiding in the plants protected by their cryptic coloration [11]. After hatching, gregarious nymphs are much more active and form dense groups that eventually constitute bands of marching nymphs [8]. Gregarious nymphs display 'hectic' behavior, with higher individual irritability and more ingestion of food [11]. When food is available and the temperature is high enough, nymphs feed almost continuously [12]. The gregarious bands display circadian cycles of activities: (1) going down their roosting plants and basking in the early morning; (2) basking in groups in the ground until body temperature is high enough to initiate marching; (3) marching and eventually jumping by late morning; (4) when the ground temperature is too high, hoppers climb on plants, jump, or hide in the shade from midday to mid-afternoon; (5) they resume marching in the late afternoon; and (6) they climb up trees or bushes at sunset to find high roosting plants to spend the night [12]. The marching bands can cover several hundreds of meters per day and display a large front of high density in a similar way as desert locust [12]. In the laboratory, Pocco et al. [9] demonstrated that crowded final instar nymphs are more active and more attracted to conspecifics than those reared in isolation, regardless of sex.
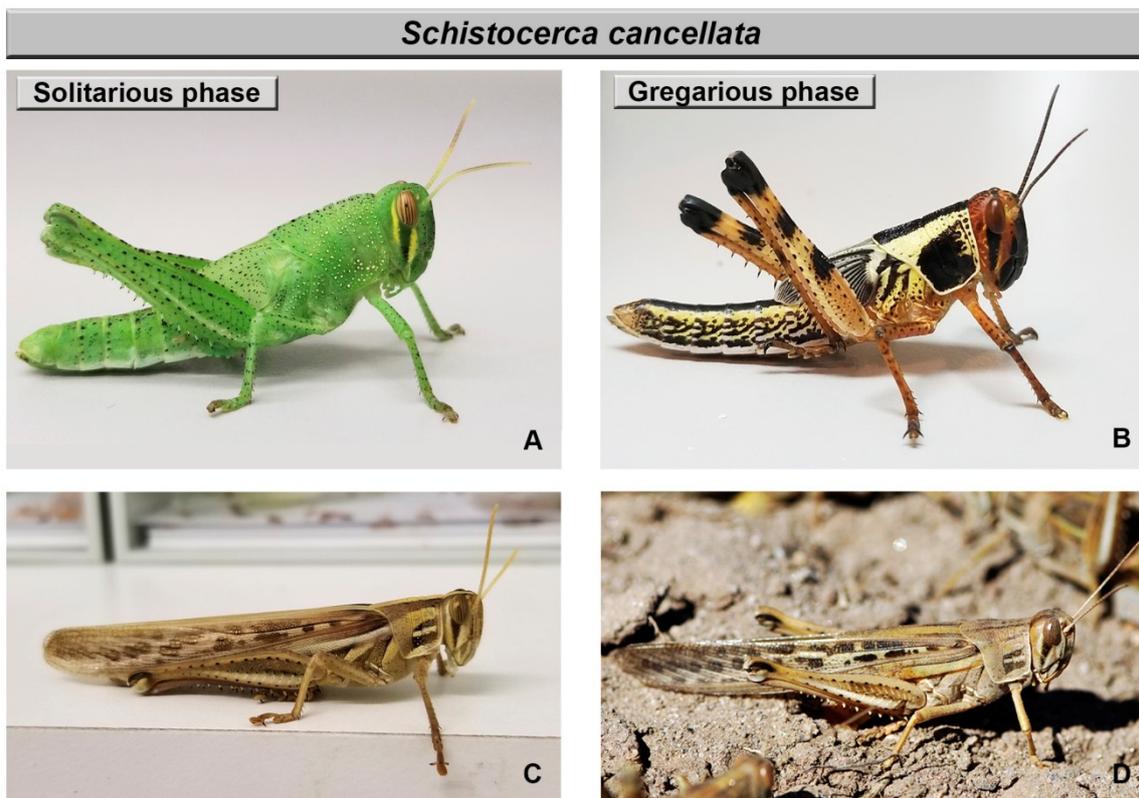
Figure 1. *Schistocerca cancellata*, (**A**,**B**) final instar nymphs and (**C**,**D**) adults. (**A**,**C**) solitarious phase (isolated locusts in laboratory); (**B**,**D**) gregarious phase (**B**) crowded nymph in laboratory; (**D**) adult female in nature). (Photographs: M. Pocco).

2.1.2. Adults

Coloration. SAL adults (Figure 1) are in general brownish, with a contrasting pattern of stripes in the pronotum, two brown dorsal bands delimited by dark brown lines, and a wide median longitudinal light-brown stripe extending from the fastigium along the tegmina. In the lateral lobes of the pronotum, there is a pattern of light brown, brown, and whitish stripes. The tegmina exhibit a pattern of dark maculae, and the hind wings are hyaline to light yellowish, with brownish veins in the remigium area. On the hind femur, there is a white stripe in the outer face, below the pinnae, and the hind tibia is purple on its dorsal face, with white spines and black tips. The coloration of SAL adults is quite similar in solitarious and gregarious individuals, although slight differences can be seen in the pattern of stripes in the pronotum. In gregarious mature adults, the contrasting coloration of stripes in pronotum is faintly evident, turning homogenously pale yellow, keeping the narrow dark brown stripes. In natural conditions, immature gregarious adults have a reddish coloration, turning to a general pale-yellow color as they mature [11].

Morphology. SAL is a large acridid: female adults range from 39 to 66 mm in length and males range from 28 to 49 mm [13]. In the laboratory, crowded male adults are significantly larger than isolated males (mean value of body length for crowded males: 58.1 mm and isolated males: 52.7 mm). The size of the female adults does not differ as much between the two density conditions (mean value of body length for crowded females: 67.2 mm and isolated females: 66.0 mm), although the head is significantly wider and the pronotum slightly larger in crowded females than in isolated ones [9].

The classic measures of phase change seen in *Schistocerca gregaria* [14] are the morphometric ratios F/C (where F is the length of the hind femur and C is the maximum width of the head) and E/F (where E is the length of the fore wing over the length of the hind femur (F)). Pocco et al. [9] found that the F/C ratio is significantly lower in crowded than in isolated adults, indicating that the head width is wider in crowded individuals, which

could be related to the voracious feeding capability of the gregarious locusts [15]. However, there was no significant difference in the E/F ratio between isolated and crowded adults.

2.2. Habitats and Feeding Preferences

As with most locusts [4,16,17], SAL outbreaks tend to originate in arid regions, which are marked by low levels of human presence, so that early outbreaks are mostly detected by government surveys. Typical habitat in the central permanent gregarization zone of Catamarca and La Rioja (Figure 2: Outbreak Area) is largely desert and semi-desert, where mountain ranges alternate with basins containing inland drainage, saltpans, extensive silt deposits, and sand dunes [18]. The dominant vegetation is wooded steppe of *Prosopis* and *Larrea* bushes, with tufts of *Sporobolus* and *Panicum* grasses or with *Atriplex* or *Suaeda* where the soil is salty [19]. The mosaic of vegetation types associated with these soil types was considered by Köhler [11,18] to be of particular importance to locusts and was termed "Acridoflora". "Acridoflora" consists mainly of annuals that spring up following rain: (Poaceae: *Bouteloua aristidoides* (Kunth), *Aristida murina* Cav., *Trichloris* sp.; Amaranthaceae: *Gomphrena martiana* Gillies; Nyctaginaceae: *Boerhavia spicata* Choisy; Portulacaceae: *Portulaca* sp.; *Heliotropium* sp.). Indeed, SAL is highly polyphagous and eats plants from many different families. The reported list for Argentina includes nearly every cultivated plant from pasture grass and cereal crops such as maize and sorghum to soybeans, peanuts, and citrus [17]. In Bolivia, the identified host range of SAL includes *Amaranthus retuflenxus*, *Sida cordifolia*, *Cassia tora*, *Nicandra physaloides*, *Panicum maximum*, *Alternanthera* sp., *Zea mays*, *Croton argenteos* L., *Cynodon dactylon*, *Schinus* sp., *Sorghum sudanense*, *Braquiaria plantaginea*, *Echinochloa colonum*, and *Digitaria sachariflora* [20,21].

Studies on field populations have revealed that SAL marching bands are carbohydrate (not protein) hungry and that access to carbohydrates is likely important for supporting long-distance migration. Teams of researchers and practitioners set artificial diets in front of oncoming bands at eight unique sites across Argentina, Bolivia, and Paraguay and found that individuals stopped and ate most often at dishes high in carbohydrates [Cease et al. unpublished data]. In the Paraguay study [22], juveniles collected from a marching band and fed artificial diets differing in a protein–carbohydrate (p:c) ratio in the laboratory had increased survival as diets became more carbohydrate biased. When fed single diets of plants that they were seen eating in the field, locusts only gained weight on the plant with the lowest p:c ratio. The plants were from the genera *Paspalum* sp., *Celtis* sp., *Mikania* sp., *Grabowskia* sp., *Prosopis* sp., and *Digitaria* sp. and one from the subfamily Celastraceae. Most of these local plants had a p:c higher than optimal, suggesting that marching locusts must actively seek out carbohydrates, or their growth and survival would be carbohydrate limited.

In contrast to the general pattern of herbivores being nitrogen or protein limited [23], SAL's carbohydrate demand and preference are similar to what has been shown for field populations of other locust species [16]. Land management practices, such as heavy livestock grazing, that deplete soil nitrogen promote outbreaks of these species by lowering plant p:c ratios [24–26]. Lower p:c diets (high carbohydrate) are likely required to support migration. Locusts rely on lipids to fuel long-distance adult flight [5,27], and while the energetic costs of locust marching have not been measured, terrestrial locomotion increases metabolic rates by 2–12-fold above resting for other insects [28,29]. In the Talal et al. [22] study, for both artificial and plant diets, SAL body lipid content increased with decreasing dietary p:c. similar to that shown for migratory locusts (*Locusta migratoria*) eating low p:c meals [30,31]. Both migratory locusts and SAL elevate CO_2 production following a low p:c meal. Talal et al. [22] showed that this is likely due to de novo lipid synthesis, as indicated by a respiratory exchange ratio above 1 (ratio of CO_2 produced in metabolism to O_2 used). Further studies on *Oedaleus* spp. in Senegal and China corroborate the hypothesis that high carbohydrate diets support locust migration [32,33].
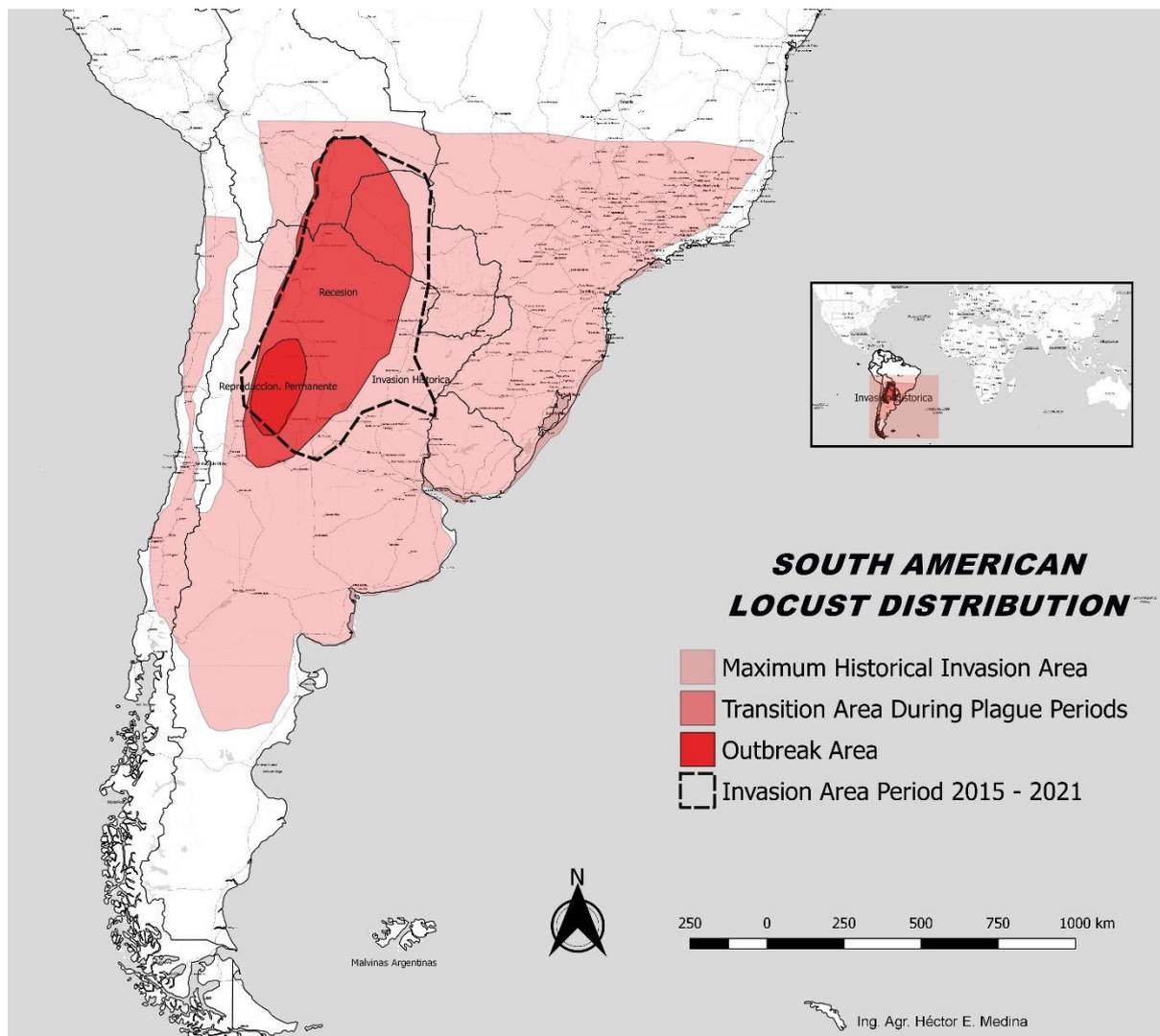
Figure 2. South American locust distribution map. Adapted from de Wysiecki and Lange, 2005.

2.3. Population Dynamics

2.3.1. Life Cycle Parameters

In natural conditions, gregarious *S. cancellata* has five nymphal instars and the total period of nymphal development is about 36–57 days [17]. Under laboratory conditions, six nymphal instars are recorded in both isolated and crowded conditions [9]. At constant 30 °C, nymphal development is 47.9 days for isolated nymphs but only 35.6 days for crowded nymphs (Table 1). As in other locusts, the number of eye stripes for both isolated and crowded nymphs is the same as the number of instars from hatching to adult [9].

Typically, there are two generations (spring and summer) per year. Adults from the second generation spend the dry season in a reproductive diapause until rains fall in spring [2,8]. During the summer non-diapause period, adults live for at least 6 weeks with maturation and laying occurring from the third week onwards when rain has fallen. During the diapause period, overwintering adults can live for up to 6–8 months from the beginning of the diapause period in autumn until the rains of the following spring [2,17]. Gregarious females lay eggs in dense groups on bare ground, laying up to six egg-pods over their lifetime, usually with 60–120 eggs per pod [17]. Egg development is continuous, and the incubation period in Argentina varies from 50–61 days for eggs laid in early spring when it is cool to 15–20 days for eggs laid in late spring or summer [2,19,34]. In Bolivia, laboratory studies found that the period from egg-laying to adult emergence of SAL in the

gregarious phase at 25 °C (normal conditions of Santa Cruz, Bolivia) is 85–95 days, with the adults living an average of a further 114 days [20].

Table 1. Summary of the main differences between solitarious and gregarious phases for the nymphal and adult stages of *Schistocerca cancellata*.

	Schistocerca cancellata				
	Solitarious Phase		**Gregarious Phase**		
Traits	**Nymphs**	**Adults**	**Nymphs**	**Adults**	**References**
Size	Final instar: males smaller; females larger	Males smaller; females similar size, narrower head	Final instar: males larger; females smaller	Males larger; females similar size, wider head	[9]
Coloration	Green, varying from light brown to light green, with small black dots	General brownish, contrasting pattern of stripes in pronotum	Pattern of striking yellow, red, or reddish orange & black	General brownish; pattern of stripes in pronotum	[9,11]
				faintly evident In nature: reddish (immature) pale yellow (mature)	
Behavior	Sedentary, disperse in the vegetation and develop in isolation	Sedentary, disperse in the vegetation and develop in isolation	Active; dense groups (marching bands)	Active; dense groups (swarms)	[9,11]
Femur hairs (%)	Higher		Lower		[9]
F/C ratio		Higher		Lower	[9]
Life cycle: N° instars	6 (in lab.)		6 (in lab.); 5 (in nature)		[9,17]
Mean duration of stage	47.9 days	87 days	35.6 days	58 days	[9,34]

In the laboratory, at constant 30 °C, the mean duration of the adult stage is about 87 days for isolated individuals compared with the significantly shorter 58 days for crowded adults [9] (Table 1). In crowded conditions, adults take about two to three weeks after molting before mating. Sanchez et al. [34] recorded 73 eggs per pod (mean value) and a mean fecundity of 161 eggs/female in crowded locusts. Based on observations made in the laboratory, the number of hatchlings per pod was higher in the crowded than in the isolated locusts (mean 85.1 for crowded; 51.8 for isolated). In the laboratory, egg incubation takes about 15–20 days.

Similar to many other locust species [4], SAL demonstrates dramatic swings in both its abundance and its occupied geographic range [3]. The population dynamics of this species are characterized as having both recession and outbreak areas sensu Uvarov [35]. In most years, there are low to moderate populations in a localized area in northwest Argentina (Figure 2) and periodic treatment of the bands and swarms that appeared in this area [2,18] helped to prevent plagues for more than 60 years [1–3]. However, SAL shows a pattern of population fluctuation that fits into Berryman's [36] sustained irruption type of population dynamics, where a period of unusually favorable conditions [36,37] can lead to rapid population increases. Once populations reach high densities, even less than ideal conditions are sufficient to maintain the population, resulting in a stable equilibrium at high densities that can result in plagues lasting many years. In the past, dense bands and swarms spread to cover more than 1.5 million km² in Argentina, Bolivia, Paraguay, Brazil, and Uruguay [1], and the current upsurge has expanded to cover a significant

proportion of this maximum area [3,20] (Figure 2). The stable equilibrium at high densities has profound effects on locust management efforts: if locust populations reach high levels, even substantial control efforts are often unable to reduce a population and end a plague unless aided by unfavorable climatic conditions [38].

Different factors influencing or determining insect outbreaks have been hypothesized including physiological [39] or top-down mechanisms [40]. Unfortunately, limited research on SAL has been carried out on the mechanisms underlying outbreaks. However, joining some known features of SAL and environmental conditions concomitant to recession and outbreak periods, a plausible hypothesis can be stated as follows.

2.3.2. The Third Generation Hypothesis

As mentioned earlier, under normal meteorological conditions, SAL has two generations [1,9]. As with the red locust *Nomadacris septemfasciata* (Audinet-Serville, 1883) in Africa and the spur throated locust *Austracris guttulosa* (Walker, 1870) in Australia [41], SAL has an adult diapause during the winter dry season. Oviposition only occurs between September and March and, then, only if rain has fallen to produce green vegetation [2]. During the June to August winter period, rainfall is very low in northwest Argentina, with an average of <7 mm per month in Catamarca and La Rioja and <15 mm per month in adjacent provinces. Rainfall during summer (December–February) is much higher, averaging > 60–90 mm/month in Catamarca and La Rioja and >100 mm/month elsewhere. Adult diapause ends around August, but adults remain immature until the first rains of the spring, which is often in October or even November. Oviposition begins a week or so after the rains, leading to the normal two (spring and summer) generations during the late spring/summer rainy period.

Importantly, rain sometimes falls during the June–September period, providing green vegetation for post-diapause adults to begin maturation and laying in September. Using a developmental model based on Barrera and Turk [42], Hunter and Cosenzo [2] found that after winter/early spring rain, three generations per year were possible: (1) early spring to early summer, (2) early summer to late summer, and (3) late summer+. In this scenario, the second-generation adults mature in late summer, just before the late March initiation of diapause, enabling a third (autumn) generation. However, only a few locations in Catamarca and La Rioja provinces were found to be hot enough to allow for these three generations [2]. Rainfall is low in Catamarca and La Rioja during winter, and for the 80 years after accurate records began for both provinces, there was significant rain (>25 mm) during any of the months between June and September for 20% of the years for Catamarca and 16% for La Rioja. Interestingly, in 1943, during the winter before the gregarization leading to the last plague of the twentieth century (1944–1954), rain fell during July in Catamarca (27.6 mm) and La Rioja (31.9 mm). Running of the model revealed that the bands of young nymphs seen during January 1944 [1] would have been nymphs of the second generation. These nymphs would have reached the adult stage by March and laid their eggs, allowing a third generation to produce the substantial number of swarms seen during winter 1944. To confirm the hypothesis of three generations and its possible importance in leading to the current upsurge, further studies should be conducted on how the higher temperatures and alterations in rainfall resulting from climate change might lead to an expanded area favorable for a third generation beyond the current Catamarca and La Rioja outbreak area. In particular, an analysis of the conditions throughout northern Argentina, Bolivia, and Paraguay that led to the resurgence of swarms in 2015 is needed.

2.4. Natural Enemies and Biological Control

SAL has many natural enemies or antagonists including predators, parasitoids, and pathogens. Numerous invertebrates, from nematodes to insects and spiders, and vertebrates, particularly insectivorous or opportunistic birds, are known to consume either embryonic or postembryonic stages of SAL [43]. Daguerre [44,45] found that *Sarcophaga* spp. parasitoid flies inflicted the highest levels of mortality in Argentina. In Bolivia, López

and Copa Bazán [20] found that natural enemies included lizards, hawks, cuckoos, spiders, and different insects such as reduvids, carabids, ants, wasps, predatory mites, and the entomopathogenic fungus *Beauveria* sp. [46]. Although such predators or parasitoids may reduce locust populations or contribute to earlier collapses [47], their actual impact has not been studied for SAL. As for other locusts [48], heavy, widespread chemical campaigns against locusts may also have had serious negative effects on natural enemies but is so far understudied.

Pathogens are the only natural enemies that have so far received some attention as possible biocontrol agents of SAL. In fact, SAL in North Argentina was among the first targets (along with Australia) of using natural enemies for control: Bruner introduced a fungus from South Africa in 1898, and the microbiologist d'Hérelle [49] applied the bacterium *Coccobacillus acridiorum*, which he had isolated from diseased locusts in Mexico. Although some good results were reported, there was little success overall [50]. Under laboratory conditions, SAL proved to be susceptible to the amoeba *Malameba locustae* and the *Entomopox* virus of *Melanoplus sanguinipes* (MsEPV) [51]. However, both pathogens are unlikely to be useful. *Malameba locustae* cysts lose viability under storage, and the MsEPV is not a native natural enemy. Species of Eugregarines (Apicomplexa) are also known to occur in SAL populations [43,52] but normally do not seem to harm the host. Among the fungi, there are old records of *Sporotrichum paranenese*, *Fusarium* sp., and *Aspergillus parasiticus* [43] and new isolates of *Beauveria bassiana* and *Cordyceps locustiphila* that are under study as possible biocontrol agents [53,54]. In China, a species of *Aspergillus* has shown high virulence against locusts [55]. The naturalized microsporidium *Paranosema locustae*, which appears to continue causing epizootics and expanding its host range in grasshopper communities of the Pampas and Patagonia [56], turned out to be not infective for crowded gregarious nymphs of SAL in the laboratory as opposed to relatively uncrowded gregarious nymphs of earlier studies [57]. It remains to be determined if *P. locustae* may prevent phase transformation when it is administered to solitary nymphs of *S. cancellata* as observed in the Migratory locust *Locusta migratoria* [58,59].

3. Management of SAL: An Historical Perspective

3.1. Early Management Efforts against SAL Plagues

The first records of locusts in Argentina date from the 1500s, with swarms damaging crops of cassava (*Manihot esculenta*) [1]. While there were reports of locusts in the following centuries, including plagues in Córdoba and Santa Fe provinces during 1833–1840 and 1844–1849 [50], detailed records of the extent of locust infestations began in the late 1800s with the continuous record of the size of locust infestations from 1897–1968 as summarized by Gastón [1]. These detailed records were a response to an increasing realization that SAL caused a great deal of damage to Argentinian agriculture, even though early damage estimates were vague and indirect. The problem led to the gradual development of specific pest control policies, characterized by a strong interventionist profile. These policies underscore SAL's seriousness and importance for the national economy [60] and led the Argentine government to create an agency to implement the first locust control campaigns. This mission was assigned in 1891 to the National Commission for Locust Extinction (CNEL) [61], which having "extinction" in its name, was based on the idea that the problem could be solved for good by a short-term campaign. In 1898, the control of SAL was declared mandatory by law (https://www.argentina.gob.ar/normativa/nacional/ley-3708-284864 accessed on 17 December 2021) and the first agricultural pest in which control was declared compulsory in Argentina. SAL was a problem of such an impact, and the difficulties experienced were so deep that the government decided in 1912 to transform this low-level and temporary office into a permanent department, named the General Directorate of Agricultural Defense, which then turned into the National Direction for Agricultural Defense and Plant Health [61]. The NDADPH was first appointed with the task of controlling SAL attacks on crops, pastures, and trees in public places, but their role widened to include all kinds of pests as agriculture advanced throughout the country.

In those first years, there was little understanding of the true nature of the population dynamics of SAL, and this contributed to a lack of effectiveness in its management. The locust problem was widespread such that, between the first detailed records in 1897 until the late 1930s, more than half of the years had SAL invasions in >20% of the whole territory of Argentina, with a maximum invasion of 57% of Argentina in 1932 [1]. There were only five years when <5% of Argentina was invaded, leading to the idea that swarms were a permanent condition of this species [18,45]. All recorded expeditions were organized during periods of large-scale locust invasions, 1908, 1917, and 1934–1936 [18,62], so studies of the gregarious swarming phase predominated. While the occurrence of a solitarious phase consistent with Uvarov's phase theory [63] began to be considered by the late 1930s, its presence was initially not generally recognized [18,62].

There were similar early misunderstandings concerning the source of invasions. In 1880 and 1892, there were observations leading to the hypothesis that invasions came from the Great Chaco in Argentina and Bolivia [63]. The belief that the "permanent region" was in northern Argentina and especially southeast Bolivia was built on the expeditions that Enrique Lynch Arribálzaga and Carlos A. Lizer y Trelles carried out in Jujuy, the northernmost province of Argentina during 1908 and 1917, respectively, coinciding with periods of very expanded invasions [1,62]. However, even though these source area ideas were erroneous, what was recognized very early was the importance of migration. D'Hérelle [49] reported widespread swarm movements: from the north towards the south in winter months and from the center of Argentina towards the north at the end of the summer months, effectively a migratory circuit later found in other locusts such as the desert locust [64–67] and Australian plague locust [68]. He mentioned that migrations were at night during the summer but only seen during the day in winter. The importance of long-distance migrations would later be further elaborated for swarm movements in the 1930s to 1950s [17] and again during the recent 2015–2021 upsurge.

Before the first systematic surveys, it was believed that SAL could reproduce anywhere and therefore every region was suspected to be a potential source of new invasions. Initially, it was also thought that SAL persisted in winter refuges, based on the frequent observations that swarms came southward to agricultural areas from northern regions. To try to locate these refuges, the Central Commission for Locust Research was established in 1933 and conducted expeditions lasting 3–4 months that explored the north and the west. These expeditions were led by three entomologists and served not only for describing dispersion paths, behavior, meteorological factors affecting swarm dispersion, feeding preferences, and natural enemies but also to test different inorganic insecticides and application equipment [69]. These expeditions were unable to find overwintering swarms, leading to the rejection of the winter refuge hypothesis [18].

During this period, there were several hypotheses concerning the wide fluctuation in the extent of the invaded area including correlations with sunspot numbers [63]. This idea may have derived from the proposition by Archibald [70] that periodical invasions of *Locusta migratoria migratoria* (L.) into the temperate zone are apparently regulated by certain meteorological conditions, which in turn seem correlated with variations in sunspots. There were similar hypotheses for the Rocky Mountain Locust ((*Melanoplus spretus* (Walsh, 1866)) in North America [71]; for *Locusta migratoria migratorioides* (Reiche & Fairmaire), still referred to as *Locusta migratoria manilensis* (Meyen) in eastern China [72,73]; and for the desert locust, *S. gregaria* [73].

The initial misunderstandings about the population dynamics of SAL combined with the widespread nature of swarming populations and an inability to locate source areas meant that management efforts during the first three decades of the twentieth century were "primitive", to use the terminology of Lizer and Trelles [62]. The locust commissions were initially established with the appointed task of exploring territories affected by swarms or bands and of recording habitat characteristics and crops affected. Control of the swarms was generally limited to treating adults settled on trees or fences. Most control measures were aimed at containing nymphal bands, a "defensive" strategy [1] aimed at preventing

bands from invading crops. The strategy was to interrupt band marching with perimetral metal barriers fixed to the ground. "Funnels" or collectors used the organized and uniform movement of the gregarized bands to direct the bands to deep trenches, where the millions of nymphs that accumulated were torched with flame throwers. Other methods included plowing to destroy the eggs, and allegedly, the adults as they lay. Hand or mechanical picking was promoted with economic compensation per bag of locusts collected. There are anecdotal records of turkeys and chickens released in the vineyards and orchards as a complementary control measure [60]. Additionally, setting fire to pastures and fallow fields was sometimes practiced but abandoned because of the low efficacy and risk of spread of uncontrolled fires [74].

During one of the long-lasting plagues in the 1920s, mechanical collection of locusts reached industrial proportions. In eastern Argentina, five hundred metal fences were installed, totaling 50 km of barriers to herd the nymphs towards corrals where locusts were sun-dried and then sold as fertilizer. The production of locust powder reached 95 million tonnes, but this practice was abandoned due to high costs [60].

3.2. The Offensive Management Period

The Locust Control Service was established in 1945 and was characterized by the heavy use of insecticides applied with blowers mounted on trucks, backpacks, airplanes, and helicopters either hired or specifically assigned to the aerial Aviation Department of the Agricultural Ministry [1]. This move was enabled by improvements in control techniques including more effective chemical pesticides (e.g., DDT) and aerial campaigns as has started in Africa [75]. While the environmental impacts had yet to be uncovered, these technical advancements allowed for the rapid treatment of large areas through offensive operations [1]. The Locust Control Service treated locusts as the upsurge increased after locusts invaded from Paraguay and Brazil in early 1945, and the infested area then expanded to 35° South by 1946–1947 [43]. In 1948, the large scale of the plague led to the formation of international cooperation between countries affected by SAL: Brazil, Uruguay, Paraguay, Bolivia, and Argentina. By 1952–1954, there was an extensive control campaign involving 12,000 tons of pesticide [17,43], and by early 1955, few locusts remained. While it was uncertain whether this decline was solely a result of the intensive treatment programs or in combination with unfavorable environmental conditions, by 1956, no gregarious locusts were detected, and this great plague period came to an end [1,3,43].

3.3. Advances That Formed the Basis for Preventive Management

The 1944–1954 plague was monitored closely not only regarding the efficiency of methods of control but also concerning the biology and population dynamics of SAL [18]. These observations led to substantial breakthroughs and to a new strategy for SAL: preventive management. The aim of preventive management was to have teams equipped for surveillance and control operations so that any gregarizing groups of nymphs or adults found early in an outbreak could be treated as a way of preventing an upsurge.

The first breakthrough was applying the phase theory of Uvarov [63] to SAL, indicating that SAL exhibited phenotypic plasticity by switching between solitarious (non-outbreak) and gregarious (outbreak) phases. The commonly encountered gregarious swarms and the scattered solitarious locusts found in northwestern drylands had been thought to be a different species [18,62]. Detailed observations in the late 1930s to early 1940s showed that they were different density-dependent phenotypes of the same species [18]. Rearing experiments demonstrated phase transformation when locusts were crowded [76]. Subsequent careful field observations revealed that the scattered locusts present during the population decline of the late 1930s started to change their behavior as numbers increased during the 1943–1944 season. Together, these advancements demonstrated that the isolated forms seen in northwest Argentina and the gregarious swarming forms of SAL were the same species [18].

The second breakthrough was that phase change (from solitarious to gregarious SAL) occurred in specific arid areas of La Rioja and Catamarca provinces [18]. This led to the realization that plagues occurred in the past because of a failure to control these newly gregarized nymphs and the resulting swarms that followed, leading to enormous costs from damage to agricultural production. The identification of localized outbreak areas meant that early targeted treatment might prevent plagues, as had been proposed by Uvarov [35] for other locusts with outbreak areas. Thus, regular surveillance for signs of gregarizing locusts and treatment of any bands or swarms found within the 100,000 km^2 outbreak area formed the basis of the preventive management program for SAL [1,18]. SAL invasions reaching Bolivia, Paraguay, Brazil, and Uruguay were correlated with swarms originating in the Argentinian outbreak area including the presence of SAL in Bolivia in 1947, 1949 [77,78] and in the recent upsurge during 2017 and 2020, where they were reported in the Bolivian Chaco region, Santa Cruz, Tarija, and Chuquisaca [79,80]. In Brazil, recorded invasions occurred in its southeast region in 1906, 1932–1933, and 1946–1948 [81], while in Uruguay, there were nine invasions that caused significant damage between 1890 and 1948 [82].

The third breakthrough was recognition that SAL had a migratory circuit. Locusts originating in the La Rioja and Catamarca regions initially as small bands and then adult groups transitioned into large migrating swarms that headed towards northern Argentina with converging winds [18]. These northward dispersions were called "concentration flights" [62], with a proposed hypothesis that summer/autumn wind currents and topography contributed to making swarms converge during this northward dispersion [11,18]. The swarms reached northern Argentina and even Bolivia and Paraguay at times. During the winter, the swarms returned south, and in the first waves of swarms, adults were reddish and tended to fly long distances following the prevailing northerly winds. As the southerly migratory movement continued, the locusts mature irregularly in pulses and disperse into ever smaller masses and begin the spring and summer breeding period.

The final breakthrough to support preventative management was uncovering the relationship between precipitation patterns and multiple SAL generations in one year. It had long been realized that SAL adults remained immature over winter, and it was thought that they matured and laid with warm weather of spring, with asynchronous and sporadic laying and hatching continuing from October to March as part of a single generation per year. However, Köhler [11,18] observed that the transition from solitarious to transiens to gregarious occurred over a period of two generations in a season. The existence of a second generation was further confirmed in February 1945, when new swarms invaded northern Argentina from Paraguay [1]. Due to a drought in the area, there was no maturation and laying despite the hot weather that was thought to lead to maturation and laying, but there was then heavy rain, which was followed by widespread oviposition and an "extraordinary quantity of nymphs" [1]. This meant not only that there was more than one generation per year [1,18] but also that rainfall was important in allowing maturation and laying, a finding reinforced by Hunter and Cosenzo [2]. Therefore, during rainy periods, adults matured rapidly and laid, allowing for more than one generation in a season, and since a female could lay 100 eggs or more, a substantial population increase was possible.

3.4. The Preventive Management Program

Uvarov [35] had suggested preventive management be implemented for locusts with outbreak areas. Such a program had begun to be implemented in the outbreak areas of the red locust, *N. septemfaciata* in Africa [83], and so, a similar preventive program was envisaged for the outbreak areas of SAL [1]. In 1954, the Service to Police and Prevent Locusts was established, which consisted of permanent scouting commissions with the aim of locating and controlling locust infestations [1,43]. At first, these commissions were deployed in an area of 300,000 Km^2, covering Catamarca, La Rioja, and adjacent provinces of northwest Argentina. Surveillance followed pre-established routes and occurred throughout the spring and summer generations. Teams were equipped for control operations so

that any gregarizing groups of nymphs or adults found could be treated [1]. Treatments were carried out usually by ground equipment such as backpack sprayers or sprayers attached to Unimogs [2] though some years had slightly larger outbreaks requiring the use of aircraft [1,2,60]. With the information gathered in the first 14 years of implementation of the preventive management strategy, it became clear that there was an area of approximately 100,000 Km^2 where the build-up of SAL population was permanent, particularly during the summer [1]. The intensity of the scouting and control process was adjusted to concentrate more on this 100,000 Km^2 area, mainly in Catamarca and La Rioja [1,2].

Following the implementation of the preventive management program in the 1950s and 1960s, outbreaks of SAL were small, with treatments on the order of a few thousand hectares or less, reaching 10,000–30,000 ha at times [1,2], much less than the hundreds of thousands of hectares requiring treatment during plagues. The resulting long recession was a complete contrast to the first half of the twentieth century when locusts were in recession for only 10 of the 55 years from 1900 and 1954 [1,2]. However, the very success of the program in containing outbreaks before they could expand to agricultural areas meant that there was little impetus for studies to increase the understanding of SAL population dynamics. Research was limited to studies by Barrera and Turk [42] on aspects of SAL biology including development rates and by Waloff and Pedgley [19], who reviewed the biology of SAL in comparison with the South African desert locust, including mention of an Argentina–Bolivia/Paraguay migratory circuit for SAL. However, the successful preventive management strategy in Argentina caught the attention of locust workers in Australia and visits to Argentina led to a detailed analysis of the plague and contrasting preventive management recession periods. Hunter and Cosenzo [2] found that, when rain fell between June and September in one or both of Catamarca/La Rioja, three generations were possible in a season, resulting in a larger than normal treatment program, which turned out to be critical in preventing the population to further upsurge to plague proportions.

In a similar way, the very success of the preventive management program led to a gradual decline in finances and resources due to the "vicious cycle" of successful prevention, leading to loss of the memory of how damaging plagues had been and gradual erosion of management effectiveness [84]. During the 1960s, there were field teams for locust surveillance and control with substantial amounts of ground equipment and access to helicopters and airplanes for treatments of larger infestations [1,60]. In 1970, Daguerre [85] warned about not enough effort being put into controlling reproduction foci before SAL reaches the reproductive stage. By the late 1980s, budget constraints led to a reduction in staff and equipment such that Hunter and Cosenzo [2] reported that, during the 1987–88 season, there were few surveys in spring and no band treatments in summer, leading to an unusually large treatment campaign against adults that included the use of aircraft. An international workshop held in February 2020 [86] confirmed the importance of a gradual reduction in financial and political support as the recession progressed, which reduced the effectiveness of the preventive management system. Participants identified the lack of a budget and a strong and continuous state policy as major explanations of the current crisis: surveillance activities became increasingly restricted in location and timing so that, when conditions favorable for an outbreak occurred, the initial outbreak populations were not located and controlled. These reductions in resources are similar to the 'vicious governance cycle' described for the desert locust [87–89]: long recessions induce a loss of interest, coordination, and institutional memory such that the human, social, material, and financial infrastructure accumulated during and immediately following plague periods, slowly decreases in the face of other political priorities.

The result was a dramatic reduction in the amount of locust survey and control [3,90–92]. Surveys were largely limited to Catamarca and La Rioja, with a dramatic reduction in access to the permanent gregarization area by closure of access trails and legal difficulties of SENASA teams being allowed to enter private property (HM, unpublished). With locusts rarely being present in numbers to cause economic damage [3], there was little institutional resistance to these increasing restrictions, thus limiting the ability of field officers to effec-

tively locate and control localized gregarious infestations [86], a key requirement of any preventive management program. Compounding these limitations was a gradual loss of institutional knowledge and experience [86], including the loss of the detailed records of the extent of bands and swarms and their treatment, so that the only records remaining were those retained in Australia by the Hunter and Cosenzo [2] study. With such decreases in knowledge and capacity to respond, it is not surprising that there was a sudden appearance of swarms in 2015 that marked the onset of the current upsurge.

4. Management under A New Plague Period

4.1. The Resurgence of SAL

The new upsurge of SAL began with the sudden appearance of in north-central Argentina during July 2015 [90,91]. In the years prior to 2015, the surveillance and control actions focused on a small area of Argentina [3], and so at present, there is no certainty about the geographical source of the original outbreak that triggered the subsequent regional emergency.

Following the appearance of swarms during July 2015, a program of widespread surveys was introduced, which found a number of swarms during spring 2015 [3]. Widespread control of nymph bands was instituted during the 2015–2016 season [90]. There was a small nymphal treatment program in Argentina during late 2016, and following sightings of swarms migrating at night in northern Salta province and at Tarija in Bolivia [HM, unpublished], many swarms were seen in Bolivia during January 2017 [91]. These northward migrations had not been documented during the 60-year period of preventive management [3].

Overall, the 2015–2021 plague was characterized by periods of breeding in Argentina alternating with breeding in Bolivia/Paraguay [3]. As a result, instead of bands and swarms being mainly limited to the outbreak area, they were present in a much larger area (Figure 2: "Transition Area During Plague Periods") [90,91] though not as large an area as sometimes occurred in the past (Figure 2: "Maximum Historical Invasion Area") [19]. During the years of migrations north (2016–2017, 2018–2019, and 2019–2020), there were generally two generations per year: a spring generation in Argentina, followed by a summer generation in Bolivia/Paraguay [3,90–92].

While there was the widespread treatment of nymphs in Argentina whenever they were present, treatment of swarms proved much more difficult: during 2015 and 2019, there was little or no treatment of swarms, and during 2017, treatments were conducted but were limited by social and governance factors [88,89]. Chemical control in horticultural areas was very difficult because the long recession period without locusts meant that there were few insecticides registered for use on such crops, and even for insecticides that were registered, strict regulations further limited their use, leading to substantial economic impacts on horticultural production [90]. When high-value fruit tree production was threatened [90,91], swarms were controlled with the decisive participation of local crisis committees that included the producers affected by the pest [86].

The new plague forced very fast learning and decision-making processes adapted to conditions that were very different from those existing in the previous plague period during 1944–1954 [60]. After 60 years, the situation changed significantly: there were many new stakeholders [93], evolving interests and priorities of citizens, farmers, and local decision-makers [86], huge changes in land use [94] particularly the extension of agricultural land [95], and greatly increased environmental concerns associated with large scale treatment programs using chemical pesticides [86]. The management program required an extremely rapid increase in tools and resources, so it was not surprising, therefore, that it took some time to facilitate the governance and oversight capable of coping with the resurgence, including the coordination of efforts and construction of links to ensure control was effective [86].

4.2. Re-Establishing a Sustained SAL Preventive Management Program

As stated by a participant to the 2020 workshop on SAL governance [86]: "the key to work with locusts in the long term is to go back to preventive management (. . .) so we don't have another crisis . . . We need preventive management, not reactive and palliative". An effective preventive strategy should be the way to manage locusts [38], but it requires first getting out of the crisis and building back a preventive system that includes international best practices.

As part of adapting SAL management to the twenty-first century, some important improvements have been made: there have been substantial improvements in the overall organization of SAL management in that collaborations between State agencies in charge of locust management, the provinces, and producers have been strongly reinforced since 2015 [84]. This improvement has mostly relied on personal commitment, "good interpersonal relationships" that emerged in the context of emergency protocols implementation and crisis committees. To maintain this commitment and improvements beyond individuals and during recession, interactions and collaboration arenas need to be institutionalized and maintained as part of a preventive management program.

To ensure the successful implementation of a new preventive management system, there also needs to be improved efficiency of data collection and analysis. In 2020, a locust alert system that notified farmers, beekeepers, researchers, and members of government about the advance of the pest was implemented. Currently, work is underway to implement this system used in Argentina throughout the region affected by SAL as it was recognized that data collection needs to be harmonized between countries to ensure that outbreaks are detected quickly and reported, so they can be controlled.

Critical to efficient preparation and planning of treatment programs is to have a better forecasting system based on an improved understanding of factors leading to outbreaks [67]. Both field and laboratory studies are needed and should utilize the latest technologies including remote sensing to accurately identify suitable locust breeding habitats and habitat conditions [96], wind analyses for migration patterns, and rates of development under different environmental conditions. Such data lead to more accurate development models that forecast the extent and timing of outbreaks so that surveys can be concentrated in areas where outbreaks are more likely. The influence of climate change on outbreaks of different locust species in the world has been debated [97], and for SAL, there needs to be an analysis of altered rainfall and temperature patterns on the location and timing of gregarization processes leading to outbreaks. However, probably, a more parsimonious explanation is that effective preventive strategies put in place for different locust species in the world in the sixties [1,83], play key roles in long recession periods. The gregarization process in SAL has been compared with that of *S. gregaria* in the laboratory [9], but there needs to be field studies such as those already conducted for *S. gregaria* [67,98–102]. A detailed analysis of ways to improve methods of treatment are required, not only an investigation of the latest chemical treatments appropriate for governments and landholders but also an integration of biological control, as has been already accomplished in Australia [103], Mexico [104], China [55], Tanzania [105], and Somalia [106] as part of complete implementation of Integrated Pest Management programs. Increasing constraints on the widespread use of chemical pesticides mean a biological alternative is essential to ensure that locusts are treated wherever they are, including in environmentally sensitive areas and where restrictions make the use of chemical pesticides difficult. To facilitate treatments in sensitive areas, the environmental sector should be more involved, including better coordination between the ministries of environment and agriculture [92].

5. Conclusions

The very success of SAL preventive management program led to less survey and control, but even more importantly, there was a virtual absence of research into the latest developments in locust biology and management. An update on locust biology is critical in view of climate change effects on rainfall and temperature, possibly altering the location

and intensity of initial SAL outbreaks, which might make regions outside the traditional provinces of Catamarca and La Rioja [1,2] important in the initiation of upsurges. Management of SAL has begun to implement some of the world's best practice, but many aspects need to be investigated and then implemented in ways relevant to the political and managerial system prevalent in the affected countries. The re-establishment of effective preventive management will rely on harmonizing coordination between Argentina, Bolivia, and Paraguay, but this "slow pace of regional coordination" encounters "obstacles coming from institutional instabilities" [86], including changing administrations. Only by "putting the three countries together" [86], through a regional plan, will an effective preventive management system be ensured and further be locust upsurges avoided.

Author Contributions: Conceptualization E.V.T., A.J.C., M.M.C., D.H.; methodology, all authors; formal analysis, all authors; writing—original draft E.V.T., M.M.C., C.E.L., M.E.P., C.P., D.H.; writing—review and editing, all authors; supervision, E.V.T, funding, A.J.C. All authors have read and agreed to the published version of the manuscript.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

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