

## Review

# Basis for the Management of *Schistocerca cancellata* (Orthoptera: Acrididae)

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## Abstract

The locust species *Schistocerca cancellata* Serville, endemic to South America, is known for its ability to form dense swarms, which reach the status of agricultural pest for several crops in southern South America. This article aimed to gather more accurate information about the history, biology, ecology, and control of *S. cancellata*, because of the 2021 invasions, which threatened to invade the Brazilian territory. During outbreak periods, swarms consume any available vegetation in the occurrence areas of Argentina, Brazil, Paraguay, Uruguay, Chile, and Bolivia. These invasions have been well documented in history, since they left deep marks wherever they went, especially in Argentina, which to this day represents the country that most accounted for agricultural losses from outbreaks. economy's main current means of control are based on pesticides, whose chemical composition induces a series of damages to health, the environment, and consequently the ecosystem. Knowing about the biological processes of this locust is an important factor in understanding how swarms form, as well as controlling them. The intergovernmental coalition shows positive results in monitoring and controlling the swarms, which, even demonstrating stability, remain under constant surveillance by competent bodies.

Key words: South American locust, swarm, invasion, agricultural pest, management

The order Orthoptera belongs to an important ramification of the infraclass Neoptera, represented by winged insects that have distinguished themselves, especially by developing specific muscles linked to the third axillary sclerite the wings to fold on the back (Bidau 2014). Orthopterans correspond to many insect species inhabiting part of the planet Earth, mainly in tropical regions. Currently, there are about 29,242 species identified in the literature, and thousands more are still awaiting scientific identification (Cigliano et al. 2022). Insects belonging to this order are popularly known as grasshoppers, locusts, mole crickets, and crickets and have inhabited the terrestrial ecosystem for at least 300 million years (Bidau 2014).

Orthopterans are hemimetabolous insects with saltatorial hind legs. Their size is relatively large, with mandibulate mouthparts for chewing, leathery forewings (tegmina), and membranous hindwings, which, when at rest, fold like a fan (Garcia 2014). The habitats of these insects are generally grasslands and native grasslands (Bidau 2014).

The order Orthoptera is subdivided into two monophyletic lineages, comprising Caelifera (locusts) and Ensifera (crickets, grasshoppers, and mole crickets). This division was scientifically established from the morphological analysis of the antennae of these insects. Individuals with reduced antennae were assigned to the sub-order Caelifera, while those with large flagellate antennae made up

the suborder Ensifera (Zhang et al. 2017). The suborder Caelifera includes about 12,397 described species (Cigliano et al. 2022) divided into the infraorders Tridactylidae (pygmy mole crickets) and Acrididae. Members of Acrididae are subdivided into seven superfamilies: Eumastacoidea, Proscopioidea, Tanaoceroidea, Pneumoroidea, Trigonopterygoidea, Pyrgomorphoidea, and Acridoidea (Song et al. 2018).

The family Acrididae comprises 38 species-rich genera, which include true locusts and grasshoppers (Guerra 2011). Among the seven superfamilies described, Acridoidea represents the largest, accounting for 11 families with approximately 8,000 species dispersed throughout the world. Locusts are heterogeneous insects. They express different shapes, sizes, and habits. They live in varied habitats, but neotropical regions are predominant. Some inhabit drier environments, such as the caatinga and Cerrado biome, while others inhabit more humid and swampy soils (Barreto and Wandscheer 2017).

For the most part, Locusts seek open forest environments such as fields, pastures, and cultivation areas and some species live in association with shrub plants, such as some bromeliads (Barreto and Wandscheer 2017). Climatic factors are strongly related to the occurrence of locusts, considering that these insects prefer mild temperatures and sites for laying eggs directly on the ground (Pocco et al. 2019). Locust phase polyphenism is a remarkable form of phenotypic plasticity (Fig. 1) in which the expression of numerous physiological, morphological, and behavioral traits occurs in response to changes in local population density (Sword et al. 2010).



**Fig. 1.** Phase Polyphenism in *Schistocerca cancellata*. The chromatic phasic polyphenism of the nymphs is reversible. The image shows the gradual change in coloration from an aggregate nymph, with bright colors (lower nymph in the hand) to a solitary nymph with a cryptic color (upper nymph in the hand). Socías, M. G. photo.

This shift to the gregarious stage occurs when certain species of locusts increase their population density, forming large swarms capable of devastating crops in short periods (Pocco et al. 2019). Large swarms of locusts indicate a possible environmental imbalance, which may have anthropogenic causes. Deforestation significantly reduces the populations of natural enemies of locusts, leading to the overpopulation of these insects in ecological areas where they occur (Barreto and Wandscheer 2017). However, some studies mention climatic factors conditioning many of the physiological activities of locusts, according to weather patterns and conditions. The phase change they undergo, which makes them a potential pest hazard, may be influenced by meteorological elements. Elevations in environmental temperature and irregular distribution of rainfall can catalyze periods of copulation and oviposition, as well as contribute to overcrowding, which is the trigger for gregarization (Morishita 1992, Retana 2000).

Only 5% of locusts have populations that can reach pest status, however, those that display gregarious behavior add up to numerous individuals per m<sup>2</sup>, allowing outbreaks that are difficult to control (Guerra 2011). However, locusts play a key ecological role in the food chain, and incorrect management to control the pest results in ecological imbalances (Costa-Neto 1998).

Among the locusts capable of forming swarms, the species *Schistocerca cancellata* Serville, 1838 (Orthoptera: Acrididae) stands out, representing a locust feared by farmers and rural residents scattered across the southern borders of the South American continent. This species, as well as the others of the genus *Schistocerca*, shows phenotypic plasticity, which is a phenomenon that provides these insects with the ability to change color when subjected to crowding. Therefore, they can express several phenotypes that transmute in response to environmental factors. *S. cancellata* has been considered one of the most problematic agricultural pests since these locusts have migratory habits that cross the international borders of Argentina, Brazil, Paraguay, Uruguay, Bolivia, and Chile, devastating most crop areas that they reach. Historical facts emphasized that the worst recorded outbreaks condemned disadvantaged rural populations to hunger and rural exodus, highlighting the governmental responsibility for vegetal health (Luna et al. 2017). This article addresses basic and applied aspects to serve as a basis for integrated management of *S. cancellata*.

## Distribution

The species *Schistocerca cancellata* is a polyphagous locust, occurring predominantly in the southern region of South America (Pelizza et al. 2017). Like other locusts, *S. cancellata* is harmless to humans and other animals, however, when aggregated, they generate significant economic losses to countries affected by the outbreaks. These losses come from the formation of dense swarms, which reach up to 25 km<sup>2</sup>. During outbreak periods, these swarms devastate numerous crops between the northern and central provinces of Argentina and neighboring countries (Medina et al. 2017).

The geographic distribution of this species varies according to population density since these insects have migratory habits (Pocco et al. 2019) and can fly up to 150 km in a day (SENASA 2018a). At each stage of life, *S. cancellata* can inhabit different countries, migrating between the territorial borders of Argentina, Bolivia, Brazil, Chile, and Paraguay (Waloff and Pedgley 1986). In addition to the direct economic losses in agriculture, the government has additional costs with the control. The government must keep the outbreaks monitored and promote the management of swarms and population foci in non-private areas (Lecoq 1991).

Locusts of this species can change between solitary and gregarious stages at any stage of their development. It is believed that the main reasons for swarming are related to environmental and climatic factors, especially periods of rainfall since dry seasons negatively affect their populations, which tend to flee (Fernandes and Pádua 2018).

Usually, *S. cancellata* has two annual generations. In Argentina, generations occur from spring to summer and from summer to early fall. Low temperatures signal the reproductive dormancy stage when locusts are ordinary in activity and live solitary. When winter temperatures are higher and rainfall is above average, a third generation may emerge, resulting in exponential population growth and increased formation of dense swarms (Luna et al. 2017).

Crops in Argentina rarely escape these massive attacks, destabilizing the country's economy since the first recorded outbreaks. In June 2020, the Ministry of Agriculture, Livestock, and Supply of Brazil (MAPA) alerted the population about the locust swarms that threatened to leave Argentina and invade the Brazilian and Uruguayan territories (MAPA 2020).

The damage was so significant that Argentina considers *S. cancellata* the most devastating agricultural pest in history (Medina et al. 2017). The National Service for Agri-food Health and Quality of Argentina (SENASA), one of the bodies responsible for monitoring the swarms in Argentina, managed to control locust swarms. However, the situation is still under evaluation, and experts guarantee that the outbreaks must remain under supervision for at least five years (SENASA 2018a).

## History

The first record of *S. cancellata* swarms was reported in Argentina in 1538 when locusts attacked cassava (*Manihot esculenta* Crantz) crops in Buenos Aires (Medina et al. 2017). Provinces located in northwestern Argentina consist of the permanent breeding area of these locusts. Therefore, they represent the regions most affected by the formation of swarms (Poffo et al. 2018). Consequently, economic losses are more significant in this region of Argentina (Medina et al. 2017).

The distribution area of *S. cancellata* covers central and northern Argentina, Uruguay, southern Brazil, Paraguay, southeastern Bolivia, and central and northern Chile. This wide distribution (almost 4,000,000 km<sup>2</sup>) corresponds, except to Chile (where *S. cancellata* remains in a solitary phase), the area of maximum historical invasion (Waloff and Pedgley 1986). The recession area of this species covers about 900,000 km<sup>2</sup>, from southeastern Bolivia and western Paraguay to northeastern Mendoza in Argentina. The area of origin of population outbursts ('outbreak area') is much smaller and extends from south-central Catamarca and La Rioja, east of San Juan, northeast of San Luis and Córdoba, and southwest of Santiago del Estero in Argentina (Waloff and Pedgley 1986, Hunter and Cosenzo 1990).

Argentina has recorded considerable damage since 1894, especially during the first half of the 20th century, when significant economic losses were reported (Köhler 1982). From 1954 to the present, demographic explosions were recorded in 1961, 1989, and 2010 (Barrientos Lozano 2011), and the last and most severe in 2015. After more than 50 yr, in July 2015, new attacks of *S. cancellata* were detected in South America, causing damage to crops and alarm in the rural population (Carrizo et al. 2015, Luna and Druetta 2015), with swarms of up to 25 km<sup>2</sup> affecting different provinces in northern and central Argentina and neighboring countries. (Medina et al. 2017, Socías 2018). Because of the most devastating outbreaks in

Argentinian history, the 2015 attack was considered the most massive since the last century, according to SENASA 2018a.

Swarms that invade Bolivia and Brazil are predominantly concentrated in the extreme south of these countries, unlike what happens in Argentina and Uruguay, where the occurrence of cases is broadly distributed throughout the territory. Records indicate that attacks have been documented in the state of Rio Grande do Sul since 1896, however, in 1905, the cases became recurrent, and swarms invaded the territory almost annually. Outbreaks of the locusts also passed through the states of Mato Grosso, Santa Catarina, Paraná, São Paulo, Rio de Janeiro, Minas Gerais, and Espírito Santo (Lima 1938). However, Rio Grande do Sul is considered the Brazilian state that most recorded damage from the passage of migratory swarms of *S. cancellata* (Fernandes and Pádua 2018).

In southern Brazil, at the beginning of the 20th century, the administrators of local colonies sent the state governor letters describing the period of despair and misery that affected the less favored rural community after the invasion of locusts. As a result of the facts, the high rate of rural unemployment reflected a great depression resulting from the recurrent invasions of locusts that consumed, above all, the alfalfa, corn, and wheat crops. The countless crop losses combined with rural abandonment further emphasized the agro-economic decline that disrupted the Brazilian economy at the time (Fernandes and Pádua 2018).

## Biology and Ecology

*Schistocerca cancellata* exhibits polyphenism which consists of carrying out coordinated changes in its usual physiological, morphometric, and molecular characteristics that vary according to population density (Pocco et al. 2019). Most of the time, this species lives scattered, at very low densities, hidden among vegetation and dry shrubs, and when disturbed, they exhibit very fast movements (Lecoq 1991). However, due to broad phenotypic plasticity, these locusts can express very subtle coloration at the solitary stage and switch to striking colors at the gregarious stage (Pocco et al. 2019).

This polyphagous species feeds on a wide array of native and cultivated plants, such as Linseed, peach, pear, plum, hazelnut, alluvium, plane tree, tomato, willow, and ornamental trees (COPR 1982). They are causing damage to wheat, barley, corn, beans, potato, cotton, sorghum, sugar cane, eucalyptus, tangerine, poplar, citrus, and pastures (COPR 1982, Duraton et al. 1987). They attack the leaves of numerous cultivated and wild plants, such as garlic, peanuts, alfalfa, oats, cassava, rice, sweet potatoes, potatoes, sugar cane, onions, rye, Citrus sp., peas, eucalyptus, fava beans, beans, lentils, flax, cassava, corn, rubber trees, wheat, wild nettles, vines, and others (Silva et al. 1968).

*Schistocerca cancellata* displays two vastly different stages; solitary and gregarious. The locusts in the gregarious phase do not necessarily form swarms. The gregarious behavior of *S. cancellata* is a genetic mechanism remarkable at certain times of the year. It consists mainly of the agglomeration of countless individuals forming a highly dense swarm (Lima 1938). The solitary stage is subtle since, during this period, the locusts move only at dawn, and the striking characteristic of this stage is the low population density (Lecoq 1991). During these periods, they inhabit parts of Argentina, Paraguay, Uruguay, and the coastal region of Chile (Waloff and Pedgley 1986).

The complete change from the solitary to the gregarious stage occurs in three or four successive generations and manifests itself in specific sites called gregarious areas. In these areas, the first swarms leave for migration. Predominantly in the northern region

of Argentina, swarms formed migrate in a joint flight from one border to another, eventually reaching Brazil (Fernandes and Pádua 2018).

Females lay their eggs inside a mucilaginous sack on the ground. After a certain period, nymphs hatch and go through five nymphal stages until they reach the adult stage. Under optimal breeding conditions, the first generation occurs in the spring, so the adults (in winter diapause) mature quickly, mate, and lay eggs in the soil and give rise to nymphs and adults of the second generation in January–February until April–May (Barrientos Lozano 2011).

The duration of the life cycle and each stage of development is variable and largely depends on environmental conditions of temperature and humidity. The egg phase lasts between 10 and 60 d under natural conditions (COPR 1982), although under laboratory conditions, embryonic development takes an average of 15 d (Sanchez et al. 1997). The amount of oviposition per female and eggs per oviposition is also highly variable. With mentions from 3 to 5 oviposition per female up to 24 and between 50 and 207 eggs per oviposition, or 161 eggs per female (Köhler 1982).

Nymph development is also variable, under controlled conditions, between 33 and 59 d until adulthood (Sanchez et al. 1997, Socías 2018). In northwest Argentina, rainfall occurs from November to March–April, allowing the development of two annual generations of *S. cancellata*. In spring, a relatively short and fast generation, and in the summer, a longer generation occurs. These adults spend the dry season (April–May to October) under reproductive diapause until spring rains (Hunter and Cosenzo 1990, Barrientos Lozano 2011). The adult stage is very long-lived, with records of 113 d (Socías 2018), during the spring generation and up to five or six months of life, the summer generation; in the latter case remaining in what is considered a status of reproductive diapause (Sanchez et al. 1997).

Displacements of *S. cancellata* are dominant at body temperatures close to 40°C. Hopping, gliding, and landing on plants are thermoregulatory behaviors to avoid soil temperatures above 50°C. Feeding was observed throughout the day with continuous, large intestinal content despite an intermittent feeding-rest-moving pattern (Piou et al. 2022).

On rare occasions with sufficient rainfall in the dry season, a third generation may occur. The pest condition is associated with mild and rainy winters, allowing the development of a third generation. Precisely, this third generation, associated with mild winters, allows the population to increase and the development of the pest status of the species in its gregarious stage (COPR 1982).

The gregarious behavior is observed when locusts are in the reproductive phase, searching for vast food and signaling possible climate changes, such as variations in temperature, relative humidity, and rainfall. Another possible factor that triggers the outbreaks is deforestation in permanent areas of this species. The destruction of habitats of natural enemies unbalances the proportion of predators required to control the great demand for locusts (Fernandes and Pádua 2018).

During the maturing season, adult male locusts secrete a pleasant pheromone reminiscent of the blooming scent. This odor is secreted by a series of individual epidermal glands, located predominantly on the dorsal side between the third and fourth tergites. Nymphs have very few scent glands in the dorsal part of their abdominal tergites. Therefore, they do not excrete a strong smell. The importance of this pheromone is associated with the maturation processes of locusts, which permeate between reproductive synchrony and maturation, and the presence of adult males among

juveniles of both sexes influences accelerating the maturation process (Hawkes et al. 1987).

Laboratory rearing of *S. cancellata* under controlled conditions has shown variations in locust development and how they respond to population density. Nymphs raised in aggregate conditions remain significantly more active than those reared in isolation. The population-level also influenced the development of different colors; for example, spherical black patterns were observed only in individuals at high population densities. While subtle, unflattering colors were evident in individuals undergoing solitary treatment. Adult males reared in agglomeration exhibited larger size than isolated ones, however, aggregate males and females did not show significant variations in size, proving that environmental factors do not significantly interfere with the size of these insects. Other influences of population density were also highlighted in laboratory rearing, such as longer, more colorful hairs in isolated nymphs (Pocco et al. 2019). The solitary individuals do not pose an agricultural threat, the confusion on identification may lead to the unnecessary spray of insecticides in the environment.

Females in seclusion showed more attraction to males, and agglomeration patterns by sex also indicated the influence of density, revealing that females remain closer to males when subjected to agglomeration, similarly, these behaviors are observed in nature (Pocco et al. 2019).

In the 2019–2020 biennium, there were important movements of *S. cancellata* populations in Argentina, Bolivia, and Paraguay towards the Southern Cone of South America, similar to those verified in the 1950s, reaching the border of Uruguay and Brazil, without, however, invading these countries (Fig. 2). Despite the similarity in movements between these two great migrations, the latter was heavily monitored and controlled by Paraguay and Argentina's extension and control services, possibly reducing the populations to levels that did not form swarms capable of producing damage or entering the neighboring countries. This latest migration is a strong indication that although there may be these movements, and the tremendous regional agricultural expansion has much more value and risks than 70 yr ago, monitoring and combating are much more efficient now, so these risks are lower than in the past.

## Morphology and Taxonomy

**Synonyms:** *Acridium cancellatum* Serville, 1839

*Acridium paranense* Burmeister, 1861

*Schistocerca paranensis*; Scudder, 1899

*Schistocerca americana paranensis*, Dirsh, 1974

*Acridium brachypterum* Phillipi, 1863

Measurements: approximately male 55 mm; female 60 mm.

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They are locusts with large, robust bodies. General body color brownish. Integument finely punctured. Filiform antennae; subglobular head; vertical front; eyes usually striped. Fastigium trapezoid, with shallow longitudinal depression. The front end is low, almost parallel, and shallowly sulcated. Pronotum tectiform; median carina obtuse and lateral carina of pronotum absent, dorsum marked by three sulci, posterior margin of pronotum rounded or largely obtuse angle. Metazone slightly longer than prozone; Dorsum of the pronotum with a yellowish or slightly brownish longitudinal stripe. A lateral lobe of the pronotum with a large brown



## South American locust migration in 1946



## South American locust migration in June 2020



**Fig. 2.** Maps showing the great migrations of *Schistocerca cancellata* in the 1940s and 2019/2020s approaching the borders of Uruguay and Brazil.

spot, interrupted in the middle by a narrow, whitish stripe. The prosternal tubercle is wide and subconical. Open mesosternal space with rectangular mesosternal lobes. Tegmina is reddish-brown with numerous irregular brown spots. The apex of the tegmina extends beyond the end of the abdomen by twice the length of the pronotum. The second pair of wings are transparent, usually slightly rosy to pale yellow. Triangular epiproct with sides excurved; apical margin obtuse angle. Presence of tympanum. Absence of stridulatory structure in the male hind femur. Male subgenital plate with bifid tip. Circi subsquare with truncate apex. The lower basal lobes of the femur are shorter than the upper ones (Dirsh 1961, 1974; Rowell 2013).

The inner side of the hind femur is uniformly colored; reddish ochre tibiae; superior carenula on the external side of the hind femur with a row of black dots. The apical spine of the hind tibia is absent. Female subgenital plate with sides excurved, obtuse angle apical margin. Ovipositor short and moderately narrow; external part

of the valves short, in lateral view, comparatively wide, and curved at the apex (Dirsh 1961, 1974; Rowell 2013).

Gregarious nymphs presented a much higher percentage of black patterns on the pronotum, wing pads, and hind femurs than solitary nymphs, which presented a low number of black patterns, restricted to small black dots distributed in a variable degree in certain structures (legs, abdomen, wing pads, pronotum) or distributed throughout the body (Fig. 3) (Pocco et al. 2019).

## Management and Control

The management of *S. cancellata* is mainly preventive, consisting of monitoring and controlling nymphs and adults. Monitoring is directed to places with a history of the presence of the pest to detect new positions in the soil, births of nymphs, or even the presence of adults. The locations of properties with the presence of the pest must be informed to the phytosanitary authorities (SENASA 2018b,

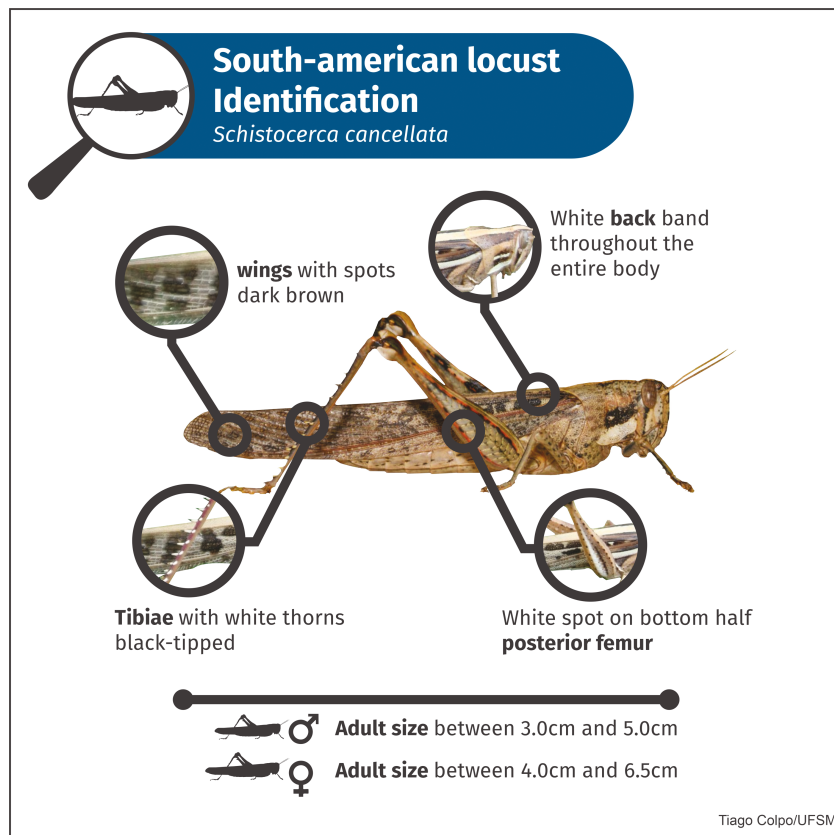


Fig. 3. Schematic illustration of morphological features for the identification of *Schistocerca cancellata*.

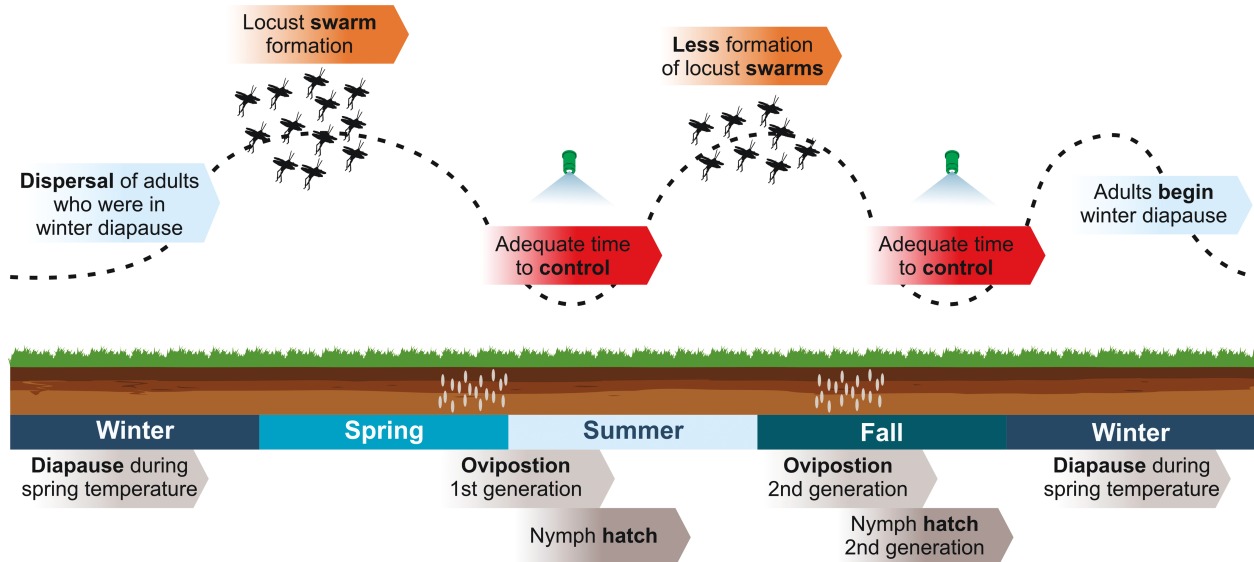


Fig. 4 Schematic illustration of guidelines for *Schistocerca cancellata* monitoring and management (Modified of SENASA 2018b).

Argentina), attaching information on the georeferencing of the site, pest development status, and the type of crop or vegetation affected.

The formation of *S. cancellata* swarms in 2015 and 2017 in different provinces of Argentina and neighboring countries, Paraguay and Bolivia, caused considerable damage to several crops, alerting and mobilizing producers and official organizations to take measures. A

locust pest was declared a national emergency (Resolution 438/2017 SENASA) in the Argentine territory. Different Technical Committees were created to combat locusts, signing agreements for cooperation and pest management between Argentine provinces and neighboring countries. To combat the pest, SENASA developed a management program that recommends monitoring and control, starting from the



The use of phytosanitary products was authorized in Argentina due to the agricultural emergency and the lack of registered phytosanitary products to control the South American locust (SENASA 2018b). Likewise, the resolution mentioned above recommends using mixtures and active ingredients according to the crop and situation (Table 1).

The Brazilian Ministry of Agriculture established the guidelines for preparing the Suppression Plan and the emergency control measures to be applied in the event of outbreaks of the pest *S. cancellata* in the Rio Grande do Sul and Santa Catarina states (MAPA 2020) and the National Plant and Seed Health and Quality Service (SENAVE 2019). The use of some chemical and biological insecticides such as *Beauveria bassiana* is authorized in Brazil (Table 2) and Paraguay (Table 3).

Exposure to pyrethroid-based substances can cause possible health risks for humans since excessive/or inappropriate contact can trigger severe intoxication, neurological and cardiac damage, and chromosomal aberrations (Santos et al. 2007). Therefore, it is essential to know the categories of authorized substances used for pest control and carefully read the labels to follow their instructions (Lopes and de Albuquerque 2018) precisely.

It is crucial to develop a regional plan among the countries of South America where an effective preventive management system is ensured and, in this way, locust outbreaks are avoided (Trumper et al. 2022).

## Final Considerations

Laboratory rearing under specific conditions proves the strong relationship between population density and phenotypic expression of this species, as well as showing that factors related to reproduction are also influenced by population density. The explanation for the outbreaks was shown to be related to climatic events, ecological imbalances, and human action.

Pest control favors agriculture, but practices using insecticides cause environmental problems, contaminate soil and water, and can trigger diseases for people and animals that have contact with these substances. In addition, insecticides must be authorized by health surveillance and used with caution, following all strict instructions to minimize environmental damage and possible diseases.

Intergovernmental communication enables more precise techniques and helps monitor cases and control outbreaks. The management of this species also emphasizes its ecological importance because *S. cancellata* is part of a food chain. Even if they reach the status of agricultural pests, they spend most of their life solitary and harmless.

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## Author Contributions

All authors conceived the idea of writing this manuscript, discussed the topic, and wrote the first draft and final version of the manuscript.

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