Analysis of the 2015–2025 upsurges of the South American Locust, *Schistocerca cancellata*: Evidence of a regional migratory circuit between Argentina and Paraguay/Bolivia

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Abstract

After an absence of almost 60 years, a major upsurge of the South American locust, *Schistocerca cancellata*, occurred in Argentina and neighboring countries from 2015 to 2020, with a further upsurge during 2024 and 2025. We analyzed locust occurrence records from Argentina, Paraguay, and Bolivia, together with temperature and rainfall data, to examine the sequence of breeding and migration during these periods. The results show repeated alternation of locust activity between Argentina and Paraguay/Bolivia, consistent with a regional migratory circuit. Detailed seasonal analyses indicate that upsurges were sustained by several generations of breeding within seasons, including asynchronous or multi-cohort development under variable rainfall conditions. While historical outbreaks originated mainly in traditional outbreak areas, specifically in the provinces of Catamarca and La Rioja in northwest Argentina, breeding now occurs over a much larger area extending from the traditional outbreak areas northwards into Paraguay and Bolivia and is likely associated with extensive clearing of the forests of the Grand Chaco. These findings indicate that the population dynamics of *S. cancellata* have changed, with implications for monitoring and control strategies, which must now operate on a broader regional scale.

Keywords

Migratory circuit, upsurges, South American locust

Introduction

Locusts are among the most devastating agricultural pests (Zhang et al. 2019). They are often found in low numbers, but when conditions are favorable, they can rapidly increase to numbers so high that they form gregarious bands and swarms that can cause substantial damage to pastures and crops. During the first half of the twentieth century, the South American locust (SAL) *Schistocerca cancellata* (Serville, 1838) was a major pest in Argentina and neighboring countries, often reaching plague proportions and forming dense flying swarms that frequently invaded the area stretching from Bolivia across to Brazil and south to central Argentina (Fig. 1) (Köhler 1962, Gastón 1969). These plagues began with localized breeding in an outbreak area centered in the provinces of Catamarca and La Rioja in northwest Argentina (Fig. 1: red circle) (Köhler 1962, Gastón 1969, Hunter and Cosenzo 1990).

Preventive operations were first implemented in Africa during the 1940's against the red locust *Nomadacris septemfasciata* (Serville, 1838) and the migratory locust *Locusta migratoria migratorioides* (Fairmare & Reiche, 1849) following the identification of their permanent outbreak areas in Africa (Uvarov 1943, Gunn 1960, Byaruhanga 1999, Rosenberg 1999). A preventive management program using similar techniques was successfully implemented against the SAL during the 1950's (Gastón 1969), which kept the pest at low to moderate numbers for many years (Hunter and Cosenzo 1990). Following Uvarov's (Uvarov 1937) proposal for preventing locust outbreaks and plagues, the program involved regular monitoring of SAL populations in Catamarca, La Rioja, and neighboring provinces and the treatment of bands and swarms encountered. Often, treatment programs were small, covering only a few thousand hectares, and even though outbreaks were larger in some years (Hunter and Cosenzo 1990, Barrientos Lozano 2011), they were always limited in extent, and SAL did not reach plague proportions for many years.

However, when locust numbers are low for substantial periods, many preventive management programs are faced with increasing budget constraints (Magor et al. 2008, Zhang et al. 2019, Gay et al. 2018, 2020), as noted in Argentina during the 1980s (Hunter and Cosenzo 1990). Trumper et al. (2022) suggested that continuing reductions in locust monitoring and control may have contributed to the failure to predict the many swarms that suddenly appeared in Santiago del Estero in July 2015, which was followed by a sustained increase in locust populations, leading to the widespread formation

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of nymphal bands and adult swarms. The SAL populations expanded such that much of the recession area was taken up (Fig. 1.), even when locust populations were low. Herein, we present the results of an examination of the sequence of generations of breeding during the years before the upsurge and since to determine whether limitations in monitoring and control or other factors contributed to the recent expansion and increase in numbers of SAL bands and swarms.

Materials and methods

We analyzed locust occurrence records taken from SENASA Argentina, SENAVE Paraguay, and SENASAG Bolivia that included data on locust stage and behavior (nymphs: usually marching bands, adults: usually flying swarms, oviposition, migration) before, during, and after the upsurges of *S. cancellata* that began in 2015. The SAL season runs from August of one year to July of the next. During autumn and winter, adults are in diapause, which ends around August (Hunter and Cosenzo 1990). Once diapause ends, adults remain immature until the green vegetation required for maturation and oviposition is present, which, in many years, does not occur until the first rains of the season in October or even November. However, sometimes winter rain provides green vegetation, allowing maturation to occur as soon as diapause ends (Hunter and Cosenzo 1990).

For this study, the timing of the development of the eggs, nymphs, and adults was determined using temperature-dependent rates of development from earlier (Barerra and Turk 1983, Hunter and Cosenzo 1990) and recent (Pocco et al. 2019) studies. For the modeling, we used temperature and precipitation records from 16 regularly reporting rain stations in areas where nymphs were frequently reported during outbreaks in the 2015–2025 study period (Fig. 1). The presence of nymphs indicated the occurrence of localized breeding that followed rainfall, egg laying, and hatching. Three of these rain stations were in Bolivia (Santa Cruz, Tarija, and Yacuiba), 10 were in Argentina (Tartagal, Oran, Jujuy, Salta, Tucumán, Santiago del Estero, Catamarca, La Rioja, Chamical, and Córdoba), and three were in Paraguay (Mariscal Estigarribia, Pozo Colorado, and General Bruguez) (Fig. 1). There are typically two generations of breeding per year, and when locust populations were low, we used the rates of development for isolated locusts (Pocco et al. 2019) during the first (spring) generation since background levels of locusts are usually isolated. Development rates for gregarious locusts (Barerra and Turk 1983, Hunter and Cosenzo 1990, Pocco et al. 2019) were used when bands and swarms were present during spring and always during the second (summer) generation, based on the assumption that locust populations would have increased after successful first-generation breeding.

Fig. 1. Regularly reporting rainfall stations in northwest Argentina, Bolivia, and Paraguay

Results

Summary of the SAL upsurges of 2015–2025.—The first major SAL upsurge in over 60 years was initially reported as the "sudden" appearance of swarms in Santiago del Estero during July 2015 (Fig. 2, blue line), and a major upsurge followed by substantial breeding in Argentina during the 2015–16 season (Fig. 2, blue line). Between 2015 and 2020, the upsurge continued at various levels: The data in Fig. 2 are indicative only of the level of infestation, as the recorded number of reports is a combination of survey effort and actual infestation level. When surveys were intense, the same adult swarm might be reported more than once as it migrated; with nymphal bands, such duplication is less likely as bands moved less and were often treated when they were seen.

Overall, the reports follow a distinct pattern in that locusts were sometimes in Argentina, sometimes in Paraguay/Bolivia, and sometimes in both (Fig. 2). On several occasions (mid 2017, mid 2019, early 2020, and mid 2020), declines in one region led to an immediate increase in the other, indicating a regular exchange of locusts between regions (Fig. 2). This 2015–2020 upsurge ended when a severe drought impacted the locust populations. The drought ended in 2022–23, and a new upsurge began in early 2024 with breeding in both regions and continued into 2025 (Fig. 2). Hence, there were two separate upsurges during the 2015–2025 period, and the origins of each, as well as the variations in breeding, are examined here in detail.

Detailed analysis of the SAL upsurges of 2015–2025

2014–15: The season leading to the upsurge.—In the years prior to the upsurge, the only significant outbreak was in Catamarca during the 2011–12 locust season, and these were treated. During 2014, the year prior to the upsurge, 900 survey stops for locusts and grasshoppers were made in the outbreak area provinces of La Rioja and Catamarca (Fig. 1) and in neighboring Santiago del Estero and Córdoba, but very few survey stops were made in the remaining five provinces in northwest Argentina. A few locust bands were reported in early 2015 in Catamarca during January (2 bands) and March (7 bands), but no other locusts were reported anywhere prior to the many swarms seen in July 2015. Bolivia received heavy rains in late 2013 and early 2014, leading to widespread flooding that would have provided ideal conditions for locust breeding, with some rains continuing in both Bolivia and Paraguay during the 2014–15 season. However, no locust surveys were conducted during this time, and no locusts were reported.

Swarms of SAL were first reported in mid-July 2015 in the northern part of Santiago del Estero province near the border with Chaco, south of Paraguay (see Fig. 1 for the location of the provinces). By the end of July, swarms were reported in Santiago del Estero as evidence of a "sudden" increase in locust numbers (Fig. 2: blue). Swarms were reported in Catamarca in early September and in Tucumán from mid-September, at which time the area with swarms included the provinces of Santiago del Estero, Tucumán, and Catamarca (Fig. 3: 2015–16, blue).

2015–16: A major upsurge.—Both Santiago del Estero and Tucumán received August rains, with oviposition seen in early October and hatchings from early November onwards. Catamarca received its first rains in late October and early November, leading to oviposition in November. Hatchings were very protracted: By mid-December, a wide range of nymphs—from recent hatchlings to mid instars—were observed. Treatments began in November, and by January, there were widespread nymphal populations in Argentina, with more than 200 foci treated during January 2016 (Fig. 2: blue).

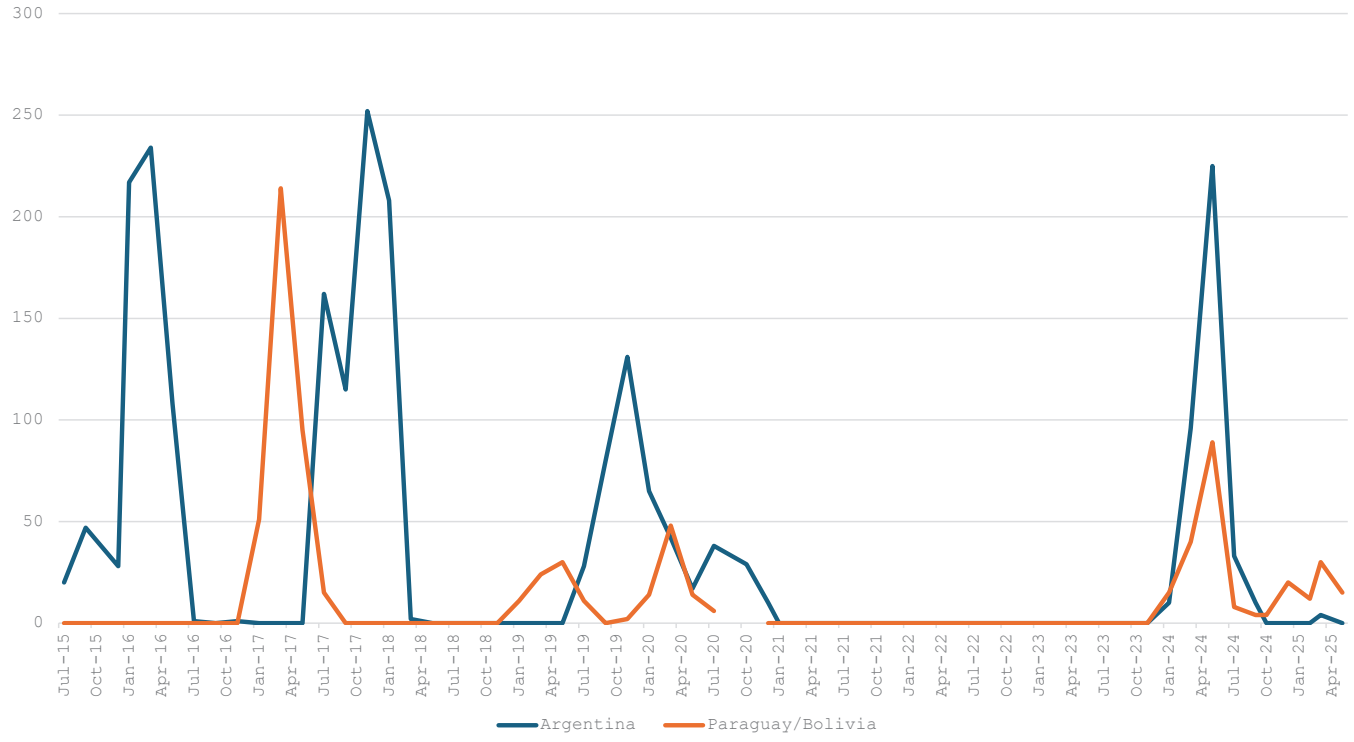

Fig. 2. Number of bands and swarms of the South American locust reported every second month in Argentina and Paraguay/Bolivia 2015–2025.

Regular rains throughout late spring and summer provided good conditions for SAL breeding, with widespread oviposition during March and a large nymphal population with nearly 250 foci treated during April 2016. These nymphs began fledging to adults in May, and after 11 swarms were treated during June, only one swarm remained by July (Fig. 2: blue).

2016–17: Locusts in Bolivia and Paraguay.—Between July and December 2016, more than 600 transect stops were made in Argentina, but only five swarms were seen: one in July, three in October, and one in November. This low overall locust population was initially thought to be a result of a very successful treatment program, but in early 2017, many swarms were reported in Paraguay and Bolivia (Fig. 2: orange). The source of this large population in Paraguay/Bolivia was at least in part a result of the locusts in Argentina migrating northwards at the end of the previous season. There were no regular surveys for locusts in Paraguay or Bolivia during winter and spring of 2016, but rains during October/ November (Mariscal Estigarribia) or October/ November/December (Pozo Colorado, General Bruguez) would have led to successful breeding. After many reports of locust swarms in Bolivia during January 2017 (Fig. 2: orange), 16,000 ha were treated during the following months. In Paraguay, nymphs and adult swarms were first reported during February, resulting in the declaration of a state of emergency and the treatment of thousands of hectares. Treatments were mainly against nymphs from late February to April, with locusts reaching the adult stage beginning in May, when there were many swarm reports (Fig. 2: orange).

2017–18: Invasion and spring breeding in Argentina.—The swarms present in Paraguay during May/June began invading Argentina in late June 2017. By late July, only a few swarms remained in Paraguay (Fig. 2: orange), but there were many swarms in northern Argentina (Fig. 2: blue), mainly in the provinces of Formosa, Chaco, and northeast Santiago del Estero. An intensive locust monitoring program was instituted that detected swarms in southern Santiago del Estero and Salta by early August, Córdoba and Tucumán in late August, and further west and south into Catamarca and La Rioja by early September (see Fig. 1 for the location of provinces). There was also a smaller migration of a few dozen swarms from Bolivia into Jujuy and northeast Salta. Overall, these migrations were like those in 2015, although they covered a more extensive area that included the provinces of La Rioja and Córdoba (Fig. 3: 2017–18, pink, compared with 2015–16, blue).

Of the more than 150 swarms reported in Argentina during July 2017 (Fig. 2: blue), 57 were treated during July, with another 46 treated during August/September. Spring rains allowed successful breeding, with many nymphal bands present until January 2018, after which numbers dramatically declined (Fig. 2: blue). A detailed analysis of the stages of development present during 2017–18 (Fig. 4) showed that following August rains in southwest Chaco, southeast Santiago del Estero, and northwest Santa Fe and September rains in Córdoba, there was some oviposition during August and September, with the first hatchings appearing during October (Fig. 4). However, most areas did not receive rain until October, leading to widespread oviposition in October and November and large numbers of nymphs from November onwards (Fig. 4). Many of the nymphs seen were treated (586 of 870 reports = 66.2%), and by February, few nymphs remained (Fig. 4). Locusts reached the adult stage from late December onwards, but only four swarms were reported in December and seven in January. Many reports of isolated adults were made during January (205) and February (183), with a decline to only

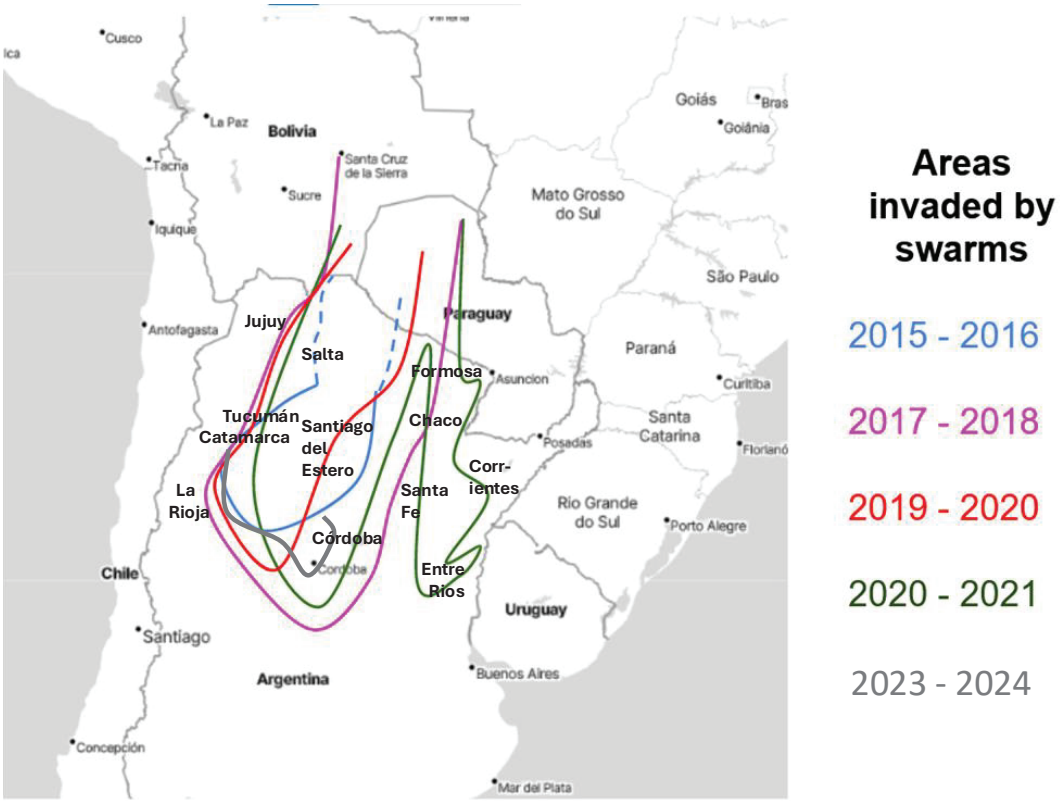

Fig. 3. Areas in Argentina invaded by swarms of the South American locust in various years from 2015–2025.

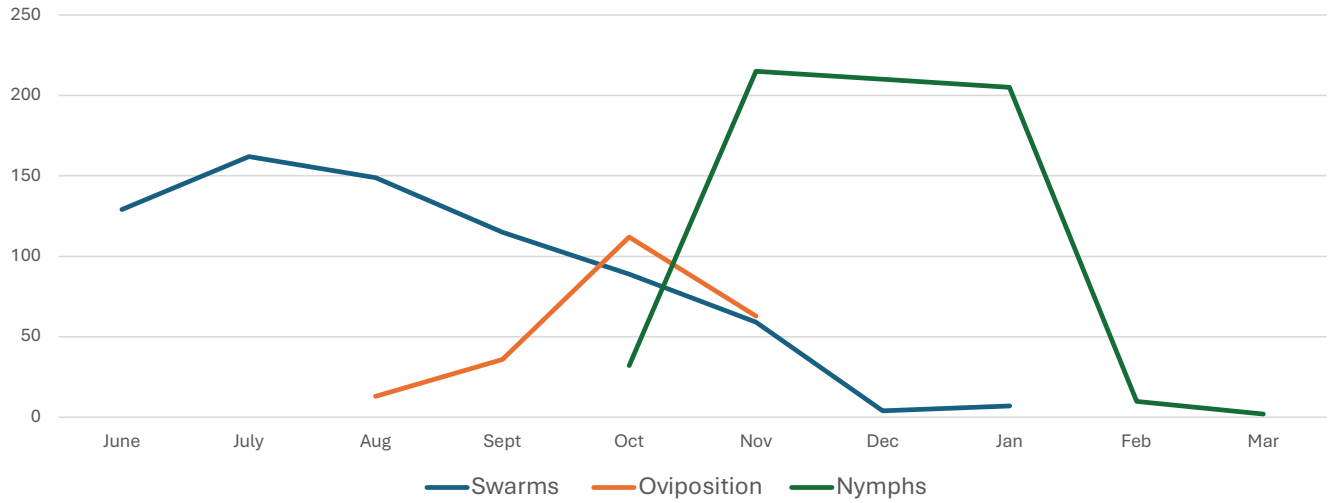

Fig. 4. Number of reports of swarms, of oviposition, and of nymphs in Argentina during the 2017–18 locust season.

eight in March. This decline in adults came about a month after the decline in nymphs: December had 210 reports of nymphs, while January had 205, with only 10 reports in February. The decline in adults about a month after the decline in nymphs combined with the presence of isolated adult locusts over a long period is consistent with the continuous low-level migration of adult locusts out of Argentina within a few weeks of reaching the adult stage. Thus, the single generation (spring/early summer) in Argentina during 2017–18 was followed by a gradual invasion of areas to the north of Argentina. The numbers would have been low in any given week, and so likely unnoticed, but substantial in total over several months.

2018–19: Locusts in Paraguay.—Few locusts were seen in most of 2018, but any locusts present in Paraguay would have received good spring rains (General Bruguez received >80 mm in September, October, and November; Mariscal Estigarribia received 77 mm in October and 209 mm in November; Pozo Colorado received >100 mm in October and November) that would have allowed substantial SAL breeding. The development models used in the present study showed that SAL would have reached the adult stage by January, and some swarms were reported in Paraguay in early 2019 (Fig. 2: orange). Oviposition was seen from early February onwards, with bands of young nymphs of the second generation present in late February and many bands present during March (Fig. 2: orange). These reached adult stage from late April into May, with 19 swarms reported during May (Fig. 2: orange).

2019–20: Invasion and breeding in Argentina.—The swarms present in Paraguay during May then invaded Argentina: As in 2017, locust swarms were reported in Formosa and Chaco in late June, and by July 2019, there were a moderate number of swarms in Argentina (Fig. 2: blue) and declining numbers in Paraguay (Fig. 2: orange). Over the next two months, swarms moved southwards such that by late August/early September, locust swarms were in southern Santiago del Estero, Tucumán, Catamarca, and La Rioja. There were also clear migrations from Bolivia, as swarms invaded northeast Salta bordering Bolivia during late July, with many swarms present in much of Salta by late August. Overall, the locust migrations and final locust distribution during 2019 were very similar to those in 2015–16 and 2017–18 (Fig. 3: 2019–20, red).

The number of swarm reports peaked in September (Fig. 5), but only four were treated. In Salta and La Rioja, the first rains of the season fell during October, leading to widespread oviposition followed by first hatchings in late October with a substantial population of nymphs by November (Fig. 5), although on a lesser scale than in 2016 and 2018 (Fig. 2: blue). Just over half of the nymphal infestations seen were treated (155 treated of 274 = 56.5%) with some swarms forming in January (Fig. 5). Elsewhere in northwest Argentina, rains did not fall until November (Tucumán) or December (Santiago del Estero, Catamarca). These rains led to an asynchronous generation in December (Fig. 5), causing a second peak of nymphs in February (Fig. 5). Most (94) of the reports of nymphs were in Catamarca, with an additional 13 in La Rioja, for a total of 107 (Fig. 5). Following substantial treatment of nymphs, only a few swarms were seen in April (Figs 2: blue, 5).

Meanwhile, there was a report of a swarm of adults maturing their eggs in Paraguay during November, and there were swarms in Paraguay and Bolivia during January (Fig. 2: orange). Regular rains in late summer allowed oviposition, and by March (Fig. 2: orange), more than 30 nymphal bands and several swarms were found in eastern Bolivia and northern Paraguay, with several thousand hectares subsequently treated. By May, some adult swarms were present (Fig. 2: orange).

2020–21: Invasion of Argentina but with limited breeding.—Swarms originating from Paraguay invaded the province of Formosa in late May and advanced into Chaco and Santa Fe before turning eastward and invading the provinces of Corrientes and Entre Rios (Fig. 3: 2020–21, green). As these provinces border Brazil and Uruguay, both countries were placed on maximum phytosanitary alert, and Brazil formally declared a phytosanitary emergency. This migratory pattern, uncommon during the previous decade, was well documented prior to the 1950s, when outbreaks of the South American locust regularly extended into neighboring Brazil and Uruguay.

Even though the situation was complicated by the COVID-19 pandemic, which led to movement restrictions, there were multiple control operations in Corrientes and Entre Ríos, and the last swarm was controlled approximately 5 km from the Uruguay River, the international border between Argentina and Uruguay. By August, however, there were substantial migrations into other areas in northern Argentina, including Chaco, Santiago del Estero,

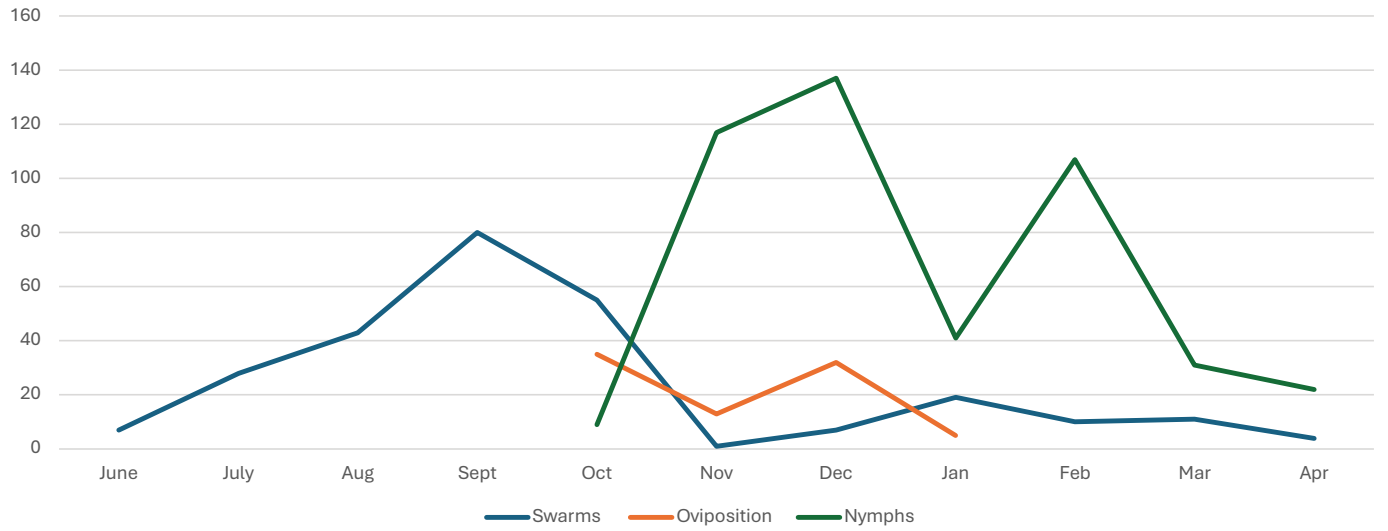

Fig. 5. Number of reports of swarms, of oviposition, and of nymphs in Argentina during the 2019–20 locust season.

Tucumán, and Córdoba, and further migrations into Catamarca and La Rioja by early October. There were also invasions of the northeast of Salta province in areas bordering Bolivia during late July and in August such that the overall pattern of invasion was like that of previous years (Fig. 3: 2020–21, green).

Five of the 38 swarms seen in July were treated, as was one of the 36 swarms seen in mid-August. By early October, the swarms seen were either in La Rioja (21 swarms) or Catamarca (eight swarms). While some rain fell in Catamarca during October, all other areas were dry; locusts dispersed such that by late October, only six swarms were seen: in Salta, Tucumán, and La Rioja. The first rains fell in these areas in mid-November, and some locust eggs did mature, with the resulting localized nymphal infestations detected in December (Fig. 2: blue) treated. No bands or swarms were reported for the rest of the season (Fig. 2).

2021–22: Severe drought.—There was a severe drought in Argentina during 2021–22, with rains beginning in November (6 stations) or December (3 stations). Few locusts were seen, with no bands or swarms reported (Fig. 2). Bolivia and Paraguay also had a severe drought: Most stations had dry periods such that the Paraná River in Paraguay was no longer navigable for moderate-sized vessels (Sigal and Desantis 2021).

2022–23: End of the drought.—While two Argentinian stations (Catamarca and Chamical) had rains in late September 2022, elsewhere, rains were again delayed and did not begin until November (3 stations) or December (5 stations). However, once rains began, they continued regularly until March/April, allowing for two locust generations. In Paraguay, rains fell in August at Pozo Colorado and in early October at General Braguez, and good spring and summer rains followed, while in Bolivia, rains fell in Yacuiba from September to March and in Tarija from December to March. In Argentina, Catamarca and Chamical received rain in late September 2022 that should have allowed spring breeding, while further rains from early December to February in Catamarca and during December/January in Chamical should have allowed a summer generation. Two generations should also have been possible at the remaining eight reporting stations that received rains from November/December to March or April. However, no locusts were reported anywhere in the region.

2023–24: Locust upsurge.—Following the two generations from 2022–23, most regions received good spring rains in late 2023, leading to an upsurge in early 2024. In Bolivia, rain began in October at Tarija and in November in Yacuiba, and locust swarms were treated in the latter area in late January/early February 2024. In Paraguay, spring and summer rains (from October onwards in Mariscal Estigarribia and General Bruguez) provided good breeding conditions leading to locust swarms in Paraguay from mid-February onwards (Fig. 2: orange). There were also good spring and summer rains (from late October/November to March/ April) at seven stations in Argentina, while two had good rains from December onwards. By February/March 2024, there were large numbers of locust swarms (Fig. 2: blue) in Tucumán, Catamarca, La Rioja, Santiago del Estero, and Córdoba such that the extent of the swarms was very similar to previous years (Fig. 3: 2023–24, black).

The widespread rains from late 2022 into 2023 and during 2023–24 should have allowed three generations of breeding over a large area in both and Bolivia/Paraguay and Argentina, and locusts were present in both regions by February/March 2024. However, some migration is likely: swarms were reported in La Rioja during February 2024, soon after the first rains of the season, so local breeding there was unlikely. By March, a major upsurge was underway, with many bands and swarms in both Bolivia/Paraguay and Argentina, resulting in about 150 treatments that month. The number of treatments increased during April and May (Fig. 2: blue, orange): initially, the infestations were mainly of second-generation bands, but many swarms formed as May progressed. Substantial treatments continued in June, and by July, the number of swarms was greatly reduced (Fig. 2: blue, orange).

2024–25: Localized infestations in Paraguay.—There were some swarms in Argentina during July of the 2024–25 season (Fig. 2: blue). However, a severe drought followed in most of northwest Argentina, with six stations going 3–5 months without significant (30 mm) rain during the six-month October to March period. The three northern rainfall stations in Argentina near Bolivia (Tartagal, Oran, Jujuy) had rains nearly every month from October to March, as did the three stations in Bolivia. In Paraguay, Pozo Colorado had rains in August and from October to March, while the other two stations had rains from December onwards. Paraguay detected adults in November 2024 and nymphal bands in December,

specifically in areas near Defensores del Chaco National Park. These reached the adult stage in January/February, giving rise to a moderate population of nymphal bands that formed swarms by May (Fig. 2: orange). These swarms subsequently began migrating southward but were controlled before they could enter Argentina.

Analysis of Catamarca and La Rioja as source areas of the upsurges.—While locusts were common in many provinces in northwest Argentina in the first half of the twentieth century (Gastón 1969), the number of bands and swarms was dramatically reduced following the introduction of a preventive management program in the 1950s (Gastón 1969, Hunter and Cosenzo 1990). Bands and swarms were largely limited to La Rioja and Catamarca provinces with localized treatments common in La Rioja (18 of 30 years) and in Catamarca (12 of 30 years) but were only occasionally conducted in other provinces: 3 years in Córdoba and 1 year in Santiago del Estero.

Hunter and Cosenzo (1990) found that during the period of plagues (1897–1954) and that of preventive management (1955–1988), SAL outbreaks began after winter, spring, and summer rainfall in either La Rioja or Catamarca or in both provinces. Prior to the 2015 upsurge, there was late winter (September) rain in Catamarca during 2010–11 (Table 1A). This was followed by a minor outbreak during 2011–12, with some bands and swarms treated during the first half of 2012. September rain also fell in Catamarca and La Rioja during 2012 (Table 1A), but there was follow-up rain in only two of the subsequent six months, and no locusts were seen. During 2014–15—the season leading to the upsurge—winter (June) rain in Catamarca was followed by November–March rain (Table 1A), but few locusts were found during surveys, even though over 1900 transects were conducted, mainly in the provinces traditionally infested with locusts (La Rioja, Catamarca) and adjacent provinces (Santiago del Estero, Córdoba). The only gregarious locusts seen in Argentina were seven treated nymphal bands in Catamarca, far fewer than could account for the upsurge.

During the 2015–20 upsurge, both Catamarca and La Rioja received winter rain during 2016–17 (Table 1B), but there were few locusts in Argentina that year, though there were bands and swarms in Paraguay (Fig. 2, orange). There was no winter rain in Catamarca or La Rioja for the remainder of the 2015–2020 upsurge (Table 1B).

Table 1. Months when Catamarca and La Rioja received >30 mm during 2010–2025. **A.** Prior to the 2015 upsurge; **B.** During the 2015–20 upsurge; **C.** Prior to and during the 2024–25 upsurge.

A.					
Season	2010–11	2011–12	2012–13	2013–14	2014–15
Catamarca	S, N, D, F	N–M	S, J, F	N–M	Jn, N–M
La Rioja	N–M	N, F	S, J, M	J–M	N–M
B.					
Season	2015–16	2016–17	2017–18	2018–19	2019–20
Catamarca	N–M	Jn, N–M	D–F	O–M	N–M
La Rioja	N–F	Jn, N, J–M	N–M	O, D–M	O–F
C.					
Season	2020–21	2021–22	2022–23	2023–24	2024–25
Catamarca	O, N, J–M	N–J, M	S, D–M	O, D, M	O, J, M
La Rioja	N–M	D–F	D, F, M	D, F, M	J

Months: Jn = June, S = September, O = October, N = November, D = December, J = January, F = February, M = March

Prior to the 2024 upsurge, there was early rain in Catamarca during September 2022 (Table 1C), and the September and December–March rains should have allowed two generations, although few locusts were seen. Rains in October and December 2024 should have allowed a third generation ahead of the upsurge in early 2024, suggesting that breeding in Catamarca may have contributed to the 2024 upsurge (Fig. 2, blue). However, the upsurge was widespread by early 2024 (Fig. 3: 2023–24, black), suggesting that breeding occurred over a large area.

Substantial clearing of forest in Argentina, Paraguay, and Bolivia.—Comparison of satellite images from 2000 (Fig. 6a) and 2019 (Fig. 6b) clearly show substantial clearing of forest in northwest Argentina and adjacent areas of Paraguay. The images show substantial clearing in the east (Fig. 6b: arrow at 1) and west (arrows at 2) of Santiago del Estero province. They also reveal substantial clearing in central Salta province (Fig. 6b: arrow at 3) and some clearing in northern Salta (arrows at 4). There is also substantial tree clearing in the areas of Paraguay bordering Argentina (arrows at 5). Thus, of the 83.3 million ha of the Grand Chaco Forest present in Argentina, Paraguay, and Bolivia in 1985, 14.4 million have been cleared for agricultural purposes (Proyecto MapBiomas Chaco 2024).

The migratory circuit of SAL.—There is clear evidence of an alteration in SAL breeding between Argentina and Bolivia/Paraguay during the 2015–25 period (Fig. 2: blue vs. orange). During 2017, 2019, and 2020, migrations southward into northwest Argentina were well documented, and there was likely a similar migration from Paraguay into Argentina in 2015.

The migrations followed the same general pattern: Swarms invaded provinces just south of Paraguay during late May (2020), June (2019), or July (2017). By August, swarms reached provinces further south (Tucumán, Santiago del Estero, Córdoba), continuing further east to the provinces of Catamarca and La Rioja either in late August/early September (2015, 2017, 2019) or in early October (2020). From Bolivia, there were small-scale migrations during 2017, and areas bordering Bolivia in northeast Salta were invaded from late July onwards during both 2019 and 2020. Overall, the pattern of invasion was similar, with a substantial overlap in the areas of northwest Argentina invaded in the various years (Fig. 3).

While the southward migrations into Argentina were often well documented, migrations from Argentina northward were not readily detected. However, there was a dramatic decrease in the locust population in Argentina in 2016 (between May and July) and 2018 (between January and March). There were many nymphs during the spring of 2018, but these were followed by only a few swarms. The many reports of isolated adults, however, imply that locusts migrated out of Argentina within a few weeks of becoming adults. The lack of detection of these northward migrations may be, in part, a result of locusts migrating in low numbers. Some flights may also have gone undetected because they occurred at night: A swarm was observed flying at night in late 2016 around the border between Argentina and Bolivia, and another swarm was observed flying at night in March 2020 around the border between Argentina and Paraguay. In addition, some of these northward migrations may have followed ecological corridors associated with the Monte de Sierras y Bolsones, allowing swarms to move through mountainous terrain in northwestern Argentina. This ecoregion covers approximately 1.7 million ha and extends parallel to the Andes from Jujuy to northern Mendoza. It is characterized by shrub-steppe vegetation distributed across intermontane valleys,

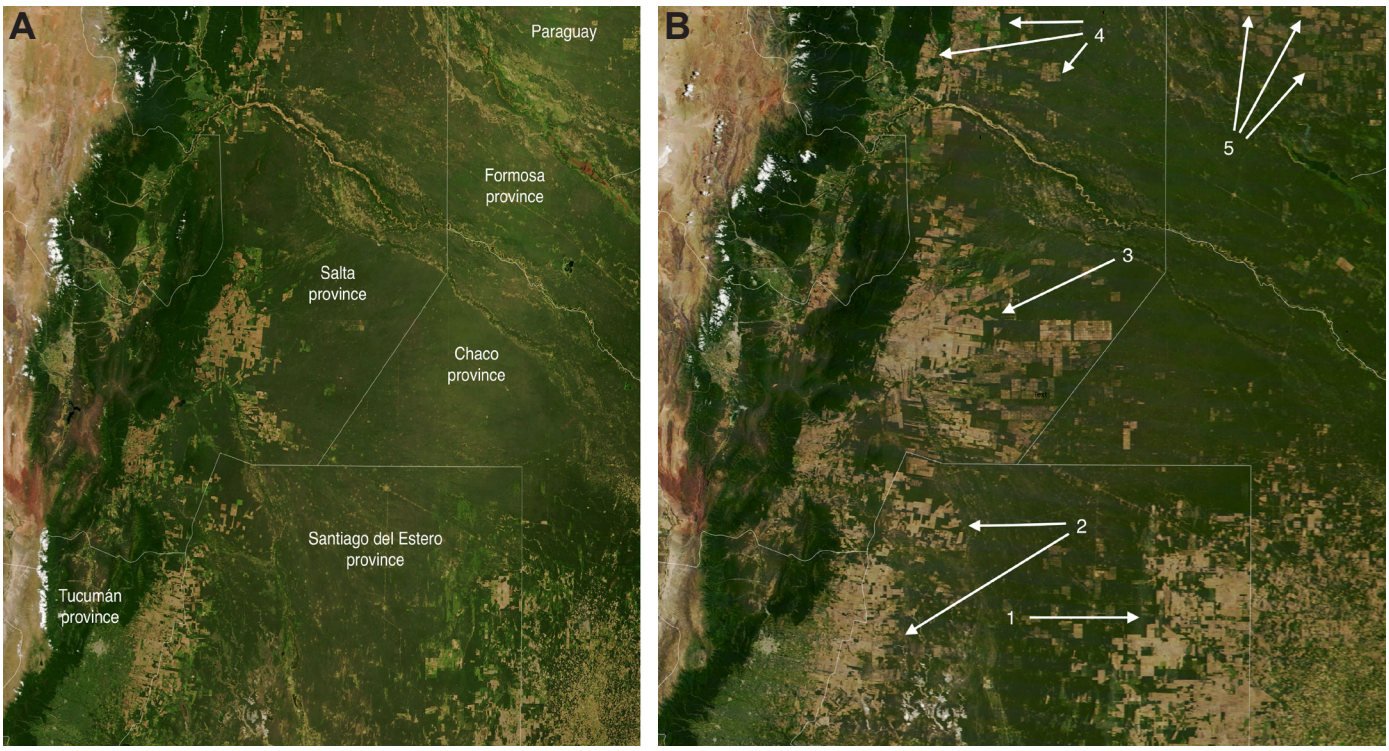

Fig. 6. Satellite images showing the loss in tree cover between 2000 (6a) and 2019 (6b) in the provinces of Santiago del Estero (Fig. 6b: arrows at 1, 2) and Salta (arrows at 3, 4) in northwest Argentina and in southern Paraguay (arrows at 5). Images used with permission from NASA Earth Observatory. (NASA Earth Observatory/NASA EOSDS Lance/)

closed basins (*bolsones)*, and mountain slopes. The continuity of this landscape may have facilitated northward migrations through suitable habitats, potentially linking breeding areas in Catamarca and La Rioja with northern regions.

Increased maximum temperatures in northwest Argentina.—While increases in temperature have been reported worldwide in recent years, of direct relevance to SAL biology is the increase in maximum temperatures during the September to March adult non-diapause period when adults mature and lay eggs, leading to nymphal hatching and development. During the September to March period, maximum temperatures increased substantially between the 1970s and recent years (Fig. 7). In the 1974–75 to 1984–85 period, maximum temperatures averaged 0.65°C below the 1981–2010 average, while between 2014–15 and 2024–25, maximum temperatures were 1.63°C above the 1981–2020 average, giving a total increase in mean maximum temperatures during the September–March period of +2.28°C.

Discussion

While upsurges and plagues of SAL were common in the first half of the twentieth century, a preventive management program begun in the 1950s successfully suppressed SAL populations through a system of regular locust surveys and treatments in outbreak areas, mainly in the provinces of La Rioja and Catamarca and adjacent Santiago del Estero and Córdoba (Gastón 1969, Hunter and Cosenzo 1990). The widespread swarm invasions characteristic of the 2015–2025 upsurge were not seen during this period, suggesting that the lack of widespread swarms prior to 2015 was real despite the lack of surveys conducted in the area.

Contributing to the dramatic change in the population dynamics of SAL from localized outbreaks in the outbreak areas of La Rioja/Catamarca to large upsurges over the much larger area from La Rioja/Catamarca northwards into Paraguay/Bolivia is the substantial clearing of the Grand Chaco forest. Scattolini et al. (2024) examined the factors associated with oviposition sites and suggested that the substantial clearing of the Grand Chaco has provided a much-expanded area for oviposition and breeding. Areas of open plain suitable for SAL now stretch more than 1000 km from the traditional outbreak areas of La Rioja and Catamarca into northern Argentina and Paraguay/Bolivia. A second factor is that within this large region, there is evidence of a migratory circuit between these different breeding areas similar to that of the desert locust (Roffey and Magor 2003), the Australian plague locust (Deveson et al. 2005), and the red locust in Madagascar (Lecoq et al. 2006). Various areas can be appropriate for SAL breeding at different times of the year, allowing continued breeding even when the traditional outbreak areas in Argentina are unsuitable. These factors taken together mean that upsurges are now a regular occurrence, such that the only time in which there were unsubstantial numbers of locust bands or swarms somewhere in the Argentina/Paraguay/Bolivia region during the 2015–2025 period was during the severe drought of 2021 and 2022 and for a year or so afterward as populations built up after the drought.

The migrations associated with the migratory circuit are clearly evident in winter, and widespread winter invasions of Argentina occurred during 2017, 2019, and 2020. These followed a similar pattern: Locust swarms from Paraguay/Bolivia invaded the border provinces of Argentina, and over several winter months, they migrated further south and west into the provinces that traditionally have had outbreaks: Santiago del

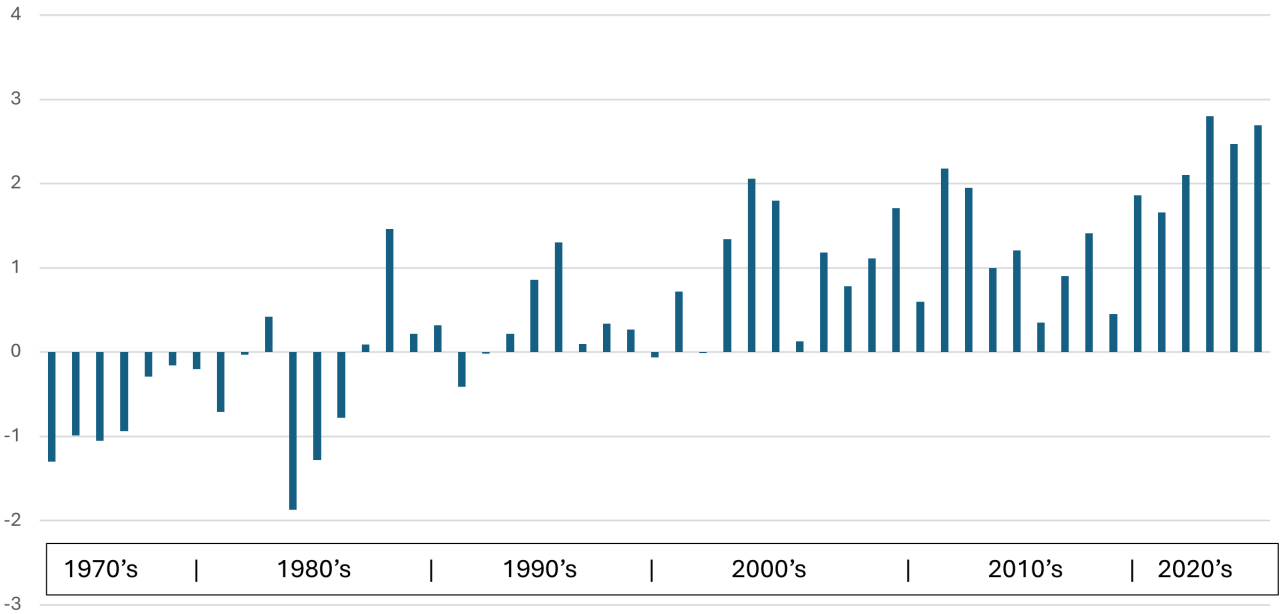

Fig. 7. Number of degrees that the mean maximum temperature during the September–March locust season was below or above the 1981–2010 mean maximum for 8 weather stations in Northwest Argentina 1974–2025.

Estero, Catamarca, La Rioja, and Córdoba. While the source of the initial populations that led to the upsurge in swarm numbers in July–September 2015 is uncertain because of a lack of surveys, the source of the locusts was likely to the north, from Bolivia/Paraguay. The southward and westward components of the winter migrations from Bolivia/Paraguay are the result of winds from the north (from the southern Amazon) and the east (from the subtropical Atlantic) being much warmer than those from the south (from Patagonia) and west (from the Andes).

The return migration from Argentina northwards is less obvious, but in two seasons (2016, 2018), substantial treatment programs against nymphs were followed by very few swarms. The presence of isolated adults suggests that adult SAL begin migrations within a week or two of reaching the adult stage, very much like the desert locust (Roffey and Magor 2003) and the Australian plague locust (Hunter et al. 1981). The spring generation in SAL is often very asynchronous: the first rains of the season that allow oviposition to being can occur at different times in different locations and when oviposition does occur, it continues for a month or more at a given location such that nymphs of a wide variety of stages can be present at the same time, leading to an extended period of fledging to the adult stage. Migrations begin a week or so after fledging, but these are so protracted that they are not noticed when leaving Argentina or when arriving in Paraguay/Bolivia.

Hunter and Cosenzo (1990) suggested that winter rain in the provinces of Catamarca and La Rioja led to a population increase caused by three generations occurring in a single season. During the first half of the twentieth century, winter rains were associated with the build up to plagues, and from the mid-1950s onwards, outbreaks were larger after winter rain but were suppressed by the preventive management program. However, the origin of the 2015–2020 upsurge was found not to be related to winter rainfall in Catamarca or La Rioja. Rather, the 2015 upsurge seems to have begun with widespread rains in the year or so before on the cleared open plains of Bolivia/Paraguay. In contrast, the 2024 upsurge seems to have developed from breeding over a much more extensive area in both Argentina and Paraguay/Bolivia.

Upsurges are now a regular occurrence; the only time there were not substantial numbers of locust bands or swarms somewhere in the Argentina/Paraguay/ Bolivia region during the 2015–2025 period was during the severe drought of 2021 and 2022 and for a year or so afterwards as populations rebuilt. The common occurrence of outbreaks is a major alteration in the overall population dynamics of SAL, which brings it closer to what used to be a feature of the Australian plague locust for which substantial treatments were a regular part of management programs (Hunter 2004). Such management programs, while able to substantially reduce damage to crops and pastures (Millist and Abdalla 2011), can prevent some plagues but not others (Hunter 2004).

The expanded spatial extent of breeding and the presence of a regional migratory circuit mean that SAL monitoring and control must operate at a broader, coordinated scale across Argentina, Paraguay, and Bolivia; this coordination is underway with the establishment of the South American Locust Regional Management Plan (Inter-American Institute for Cooperation on Agriculture [IICA 2021]). Within this framework, there must be cross-border information sharing and coordinated survey and control using updated methods and technologies, including drones and remote sensing. Data on locusts and meteorological conditions need to be integrated into GIS-based approaches that account for the different ways in which outbreaks can develop. These data can then be used in locust development models to forecast the timing of the various stages of development: these forecasts need account for the recent increases in maximum temperatures during the locust season that can speed up development, balanced by solitary SAL having longer development times (Pocco et al. 2019). Such modelling could provide essential support for decisions on the timing and targeting of survey and control operations within the region.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text.