

## Importance of solitary desert locust population dynamics: lessons from historical survey data in Algeria

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### Abstract

The desert locust, *Schistocerca gregaria* (Forskål) (Orthoptera: Acrididae), is a major pest and well known in its gregarious phase. However, it is not well understood during recession periods, when the solitary phase populations are discrete. Nonetheless, these populations are at the origin of the invasions when ecological conditions become favourable. This lack of knowledge of the solitary phase individuals impedes effective preventive management of this pest. Archive data collected in Algeria from 1980 to 2011 were used to analyse solitary population dynamics across the Algerian Sahara where some outbreak areas are located that play a major role in the invasion process. The results confirm previous empirical observations on solitary population dynamics. First, a clear difference could be documented between the northern and southern Saharan regions of Algeria concerning the locust dynamics and the impact of environmental conditions. The importance of runoff was clear to create suitable habitats over a long period and to very distant places from rainy areas. Second, a link, on an annual basis, between green vegetation and presence of solitary locusts was found. Third, statistical relationships between various locations demonstrated a clear regional dynamics. Our study confirmed the importance of migrations of solitary populations among Algerian regions and more generally within the recession area of this species. The operational implications of these findings are multiple. First, they confirm the need of a flexible and scalable preventive system during the year, from 1 year to another and with a clear distinction between the northern and southern Saharan areas of Algeria. Second, they also confirm the necessity for the inclusion of wadis and soil moisture estimations from remote sensing in geographic information systems for preventive management. And third, they clearly illustrate the importance to target solitary locusts for more efficient preventive survey operations.

### Introduction

To implement a coherent control strategy against any pest species, knowledge on population dynamics is of prime importance. For the desert locust, *Schistocerca gregaria* (Forskål) (Orthoptera: Acrididae) – a major pest whose invasions start in the desert areas of Mauritania to India – population dynamics seem generally well known and many authors have described their main processes

(Waloff, 1966; Uvarov, 1977; Magor, 1994; Roffey & Magor, 2003). The desert locust presents a phase polyphenism phenomenon, developing various and reversible aspects according to population density (Pener & Simpson, 2009). At low density, they are in solitary phase, typical of recession periods. At high density, they transform into ‘transiens’ and ultimately into a gregarious phase whose swarms may cause extensive damage during invasions. Locust phase polyphenism is continuous and phase characteristics can be shifted to both directions, reversibly, and at any development stage (Pener, 1991).

Desert locust is considered an international issue with major economic, social, and environmental impacts

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(Lecoq, 2004). The costs of locust control campaigns are generally estimated in hundreds of millions of dollars. Large amounts of chemical insecticides are used for control operations and can result in serious damage to the environment. The consequences of the invasions can be disastrous for food security of many states in affected areas in Africa and Asia. During the 2004 invasion in the Sahel countries, at least 8 million people have suffered destruction of all or part of their food crops (Brader et al., 2006). The social consequences are visible on the long term, and 20 years after the 1987–1988 invasion, it was still possible to find a strong impact of the income shock on the educational outcomes of children living in affected areas of Mali (De Vrejer et al., 2014).

The risk of destructive large swarms can be effectively managed by the application of a preventive strategy based on the monitoring of outbreak areas (Magor et al., 2008; Sword et al., 2010). This strategy, recommended as early as 1960 (FAO, 1968, 1972; Hafraoui & McCulloch, 1993; Krall et al., 1997; van Huis et al., 2007; Magor et al., 2007), continues to be the subject of criticism and discussion on the best timing of control operations (Joffe, 1995; Symmons, 2009). However, prevention remains the current strategy and its implementation is a probable factor in the reduction in the frequency, duration, and magnitude of invasions (Lecoq, 2001, 2003; Magor et al., 2008). In parallel, the areas to be monitored have been reduced considerably, from 31 million km<sup>2</sup> of invasion area to 15 million km<sup>2</sup> of recession area and then to the 250 000 km<sup>2</sup> of outbreak areas (Sword et al., 2010).

During recession periods, the main concern of monitoring locust units is to localize as quickly as possible outbreaks of desert locust populations, optimizing at the same time the survey itinerary of the field locust officers (van Huis, 2007; van Huis et al., 2007). They focus on breeding areas where ecological conditions may become temporarily favourable and can promote an invasion. The early localization of these breeding areas is critical for effective preventive treatments before the first gregarious swarms disperse (Magor et al., 2008). This monitoring implies detailed knowledge of solitarious populations and of environmental factors that could explain their presence. Unfortunately, this knowledge remains fragmentary and penalizes the efficiency of monitoring operations and prevention (Uvarov, 1977).

Solitarious locust populations, during recession periods, are scattered in the immensity of the Sahara and thus difficult to detect and to study. They remained unknown for a long time and priority has been given to gregarious populations and their control. The assumption was – and

occasionally continues to assert – that these solitarious populations were of low numbers and sedentary, as opposed to the numerous and highly mobile gregarious populations (Sword, 2008). Their role in the genesis of invasions has long been denied (Pasquier, 1942; Rainey, 1963, 1971) and, during recession periods, large areas of the Sahara desert have even been supposed to be empty of locusts (Waloff, 1966).

Gradually the concept of the solitarious phase has changed dramatically. Nowadays, we know that these solitarious populations actively migrate at night, with most large-scale migration taking place by single individuals (Matthews & Matthews, 2009). They probably cover hundreds of kilometres between complementary areas for breeding (Waloff, 1966; Roffey & Magor, 2003). These solitarious populations are probably much more abundant than previously believed (Chapuis et al., 2014, 2015). Their role in the invasions' genesis is crucial (Lecoq, 2001, 2005; Magor et al., 2008), as it was also demonstrated in other locust and grasshopper species (Lecoq, 1975, 1978). Lastly, the main factor favourable to initiate an invasion is a succession of heavy rainfall over very large areas, allowing solitarious locust populations to reproduce intensely (Waloff, 1966; Duranton & Lecoq, 1990; Symmons & Cressman, 2001).

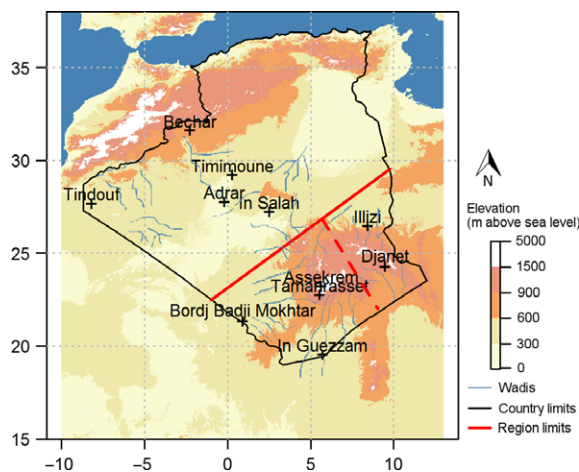
Any information on the dynamics of these solitarious populations is crucial for designing effective management strategies, even though the locust problem is now better controlled and the invasions are shorter and rarer than before the 1960s. Because so few field studies were specifically dedicated to solitarious populations, many assumptions remain (Roffey & Magor, 2003). Research effort recently focused on solitarious populations (Lecoq, 2001, 2005; Sword et al., 2010) and a lot of information has been accumulated through the patient and steady effort of locust centres distributed throughout the countries with outbreak areas. The resulting large databases – initially made for operational purposes and not for research – are exploited. They have already helped to better assess the distribution of these solitarious locust populations in the Sahara (Popov, 1997; Guendouz-Benrima et al., 2007; Babah Ebbe, 2008; Piou et al., 2013) or to evaluate the population density at which gregarization could happen (Cisse et al., 2013). The objective of this study is to identify the respective roles of environmental and intrinsic factors explaining local and regional dynamics of solitarious and transiens population development in recession periods. On the basis of the Algerian locust monitoring archives, we propose analyses at monthly and yearly scales to evaluate the influence of environmental conditions on these dynamics.

## Material and methods

### Study area and desert locust habitats

This study was performed in southern Algeria, a vast Saharan zone harbouring potential development, breeding, and gregarization areas of the desert locust. Since 1965, more than 90% of the reports of presence of the desert locust have been carried out therein (the others being in the Atlas and the northern coast of the country). This Saharan region covers more than 80% of the area of Algeria, about 2 million km<sup>2</sup>, and consists mainly of regs (plains largely covered by gravel), ergs, oases, and mountains. The north is bordered by the mountains of the Saharan Atlas culminating at 2 336 m in the Djebel Aissa. In the centre, the region from Tindouf in the West to In-Amenas in the east through Adrar and In Salah has an average altitude of 800 m. In the south, there is the Hoggar Mountains, which rise to 2 918 m near Tamanrasset and the Tassili n'Ajjer massif with 2 254 m near Djanet. In the extreme south, the massif of Adrar des Iforas continues into Mali (Figure 1).

Across the entire study area, climate is Saharan, characterized by its aridity: very low rainfall, high temperature – often 40–45 °C, sometimes almost 50 °C –, and high daily thermal amplitude. The mean annual rainfall (1965–2013) is between 88 mm in the north (Bechar) and 16 mm in the south (Djanet). Throughout the region, habitats of gregarization for desert locust are almost always associated with networks of wadis coming from the Saharan mountains (Hoggar, Tassili n'Ajjer, Adrar des Iforas, southern piedmont of the Atlas). They are located along the wadis



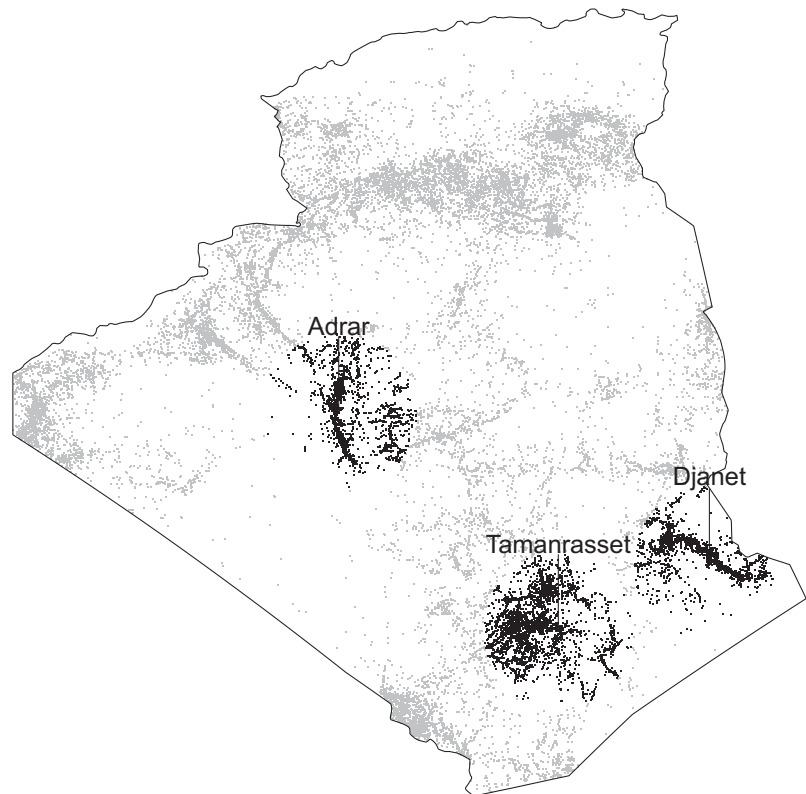
**Figure 1** The 11 weather stations of the Algerian territory used in the study and limits of three regions as reflected by the monthly analyses (see Table 1). [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

with silty clay soil covered with some sand, holding moisture pretty well, and allowing the locusts to lay eggs over a long period of time. The necessary moisture for breeding results both from rainfall and runoff from the higher areas, where local orographic rainfall complements the scarce seasonal rains (Popov et al., 1991). In some cases, the drainage basin brings water to gregarization habitats localized several hundreds of kilometres from the rainfall. In some other cases, the accumulated water reserves are considerable and remain available for several months (Lecoq, 2012). When water supply is sufficient, the desert locust will find optimal development conditions in these habitats. This is true both for feeding [e.g., *Schouwia purpurea* (Forssk.) Schweinf., *Tribulus spec.*] and for sheltering [e.g., *Acacia ehrenbergiana* Hayne, *Acacia tortilis* (Forssk.) Hayne] (Duranton et al., 2012). These habitats may harbour outbreaks and trigger gregarizations, they are the subject of a regular monitoring as part of preventive operations (Cressman, 2001; Lecoq, 2003, 2005).

### Data collection

In Algeria, the National Institute of Plant Protection (INPV) conducts regular monitoring of the desert locust populations whose main focus is the areas containing locust breeding sites, in the southern part of the country. The potentially favourable areas for locusts are explored according to a procedure and a standardized methodology recommended by FAO (Cressman, 2001). The collected information includes the geographical coordinates of the observation site, data on locusts (density, behaviour, development status...), as well as environmental conditions (vegetation, soil moisture...). The field information is stored in a central database RAMSES (Reconnaissance and Management System of the Environment of *Schistocerca*) set up by FAO-DLIS (Desert locust Information Service) in all countries concerned with preventive control (Cressman & Hodson, 2009).

The data used in this study were extracted from the Algerian RAMSES database, hosted at INPV in Algiers. It contains more than 39 000 recordings on desert locusts and their habitats, collected during field surveys over a period of 48 years, from 1965 to 2013. However, all the variables are not always recorded at each observation site. Thus, in addition to the observation date and to the location of the survey site, we only used the data about presence/absence and phase (solitary, transiens, gregarious) of locusts, as well as the phenological state of vegetation (recorded for ca. 60% of surveys, other environmental variables being recorded in less than 30%). Phase statuses of locust populations were recorded by survey teams following FAO guidelines (Cressman, 2001) based mainly on locusts morphology, coloration, behaviour, and overall



**Figure 2** Sites surveyed throughout the Algerian territory from 1980 to 2012 and those selected for the annual analyses (in black) around the three weather stations Tamanrasset, Djanet, and Adrar.

population dynamics. Meteorological data for the same period were recovered from the desert locust Meteorological Centre in Tamanrasset for the only 11 weather stations of southern Algeria (Figure 1) where meteorological data were well informed since 1980. For consistency in quantity and quality of data and for data continuity over the years, we selected the locust and weather information from 1980 to 2012 (which represents 32 622 records, for as many field surveys with 5% of them finding solitarious and 4% of them finding transiens locusts).

#### Data analysis

The analysis was conducted in two steps, first on a monthly basis for surveys at different distances around each of the 11 weather stations, and then on an annual basis for three study areas identified from the first analysis.

#### Monthly analysis

We focused first on the dependent variable of total number of observations of solitarious or transiens locusts in a given month ( $Y$ ). For each of the 11 weather stations, we looked on all survey points lying within a radius of 20, 30, 40, etc., up to 500 km around its geographical position, to take into account the flows of water in the wadis. These selections of nested dots generate sets of data used in

repeated analyses, for each distance, to estimate the factors influencing locust dynamics. At each distance, separate negative binomial regression analyses were conducted to assess the role of the rain (monthly data of weather station,  $P$ ) and of temporal autocorrelation of locust dynamics in the number of reports of solitarious or transiens hoppers or adult locusts ( $Y$ ). Vegetation could not be considered at the monthly level as the counts of locust reports and the proportion of observations with green vegetation are both related to the number of surveys and therefore highly correlated. In the end, the full statistical model can be written as follows:

$$\log(Y) \sim aP + bP_{-1} + cP_{-2} + dP_{-3} + eY_{-1} + fY_{-2} + gY_{-3},$$

where  $a$ ,  $b$ ,  $c$ ,  $d$ ,  $e$ ,  $f$ , and  $g$  are parameters of the regression to be adjusted, and subscripts  $-1$ ,  $-2$ , or  $-3$  correspond to data shifted 1, 2, or 3 months back, respectively.

In total 125 models were adjusted from combinations of the variables of the complete model. Among these 125 adjustments, the model with the smallest Akaike information criterion (AIC; Akaike, 1973) – that is, the most explanatory and most parsimonious – is selected for each distance and each station. With the statistical models selected at each distance, a gradient of the use of variables

and of their significance to explain  $Y$  were obtained and analysed for each station. To synthesize this information, significant relationships appearing or disappearing in <30 km along these gradients were not interpreted. The results of these analyses indicated at what scales of distances and in which direction (positive or negative effect) the reports of solitarious or transiens locusts were influenced by rainfall and local locust dynamics. This entire monthly analysis was repeated for the dependent variable ( $Y$ ) of the total number of observations of solitarious hoppers and of transiens hoppers in a given month.

### Annual analysis

From the monthly analyses, three regions of Algeria were identified for their differences in locust dynamics. The weather stations of Tamanrasset, Adrar, and Djanet were retained for the annual analysis based on their representativeness of these three regions. Survey points located within 200 km (half the minimum distance between these three stations) around each of these stations were processed to generate five variables for each region: (1) total of annual reports of solitarious desert locusts, hoppers, or adults (solitarious reports, NS); (2) total of annual reports of transiens desert locusts (transiens reports, NT); (3) total annual rainfall (P); (4) annual number of months when rain was recorded (number of rainy months, MP); and (5) annual proportion of reports where green or greening vegetation was observed (green vegetation, V). A global variable for an invasion situation in Algeria (denoted I) was also noted if more than five swarms in the three regions were reported. Thus, the years 1987, 1988, 2004, 2005, and 2012 were considered as 'invasion', the others as 'non-invasion'.

Both locust variables for each region (e.g., TNS = number of solitarious reports around Tamanrasset, or ANT = number of transiens reports around Adrar) were considered as dependent variables, possibly explained by (1) other variables in the same region; (2) locust variables of the two other regions; and (3) the global invasion variable. For example, to explain TNS, we considered as explanatory variables TNT, TP, TMP, and TV (where the first T always refers to Tamanrasset) and I, ANS, ANT, DNS, and DNT (where A and D refer to Adrar and Djanet, respectively). To account for the potential effects of temporal autocorrelation and cross-correlation, locust variables were also used as explanatory variables but shifted by 1 year (TNS<sub>-1</sub>, TNT<sub>-1</sub>, I<sub>-1</sub>, ANS<sub>-1</sub>, ANT<sub>-1</sub>, DNS<sub>-1</sub>, and DNT<sub>-1</sub> in the example). Thus, for each of the six locust variables to be explained, we had 16 potential explanatory variables. To avoid the effects of interactions between explanatory variables that can appear in the construction of over-parametrized statistical models, we focused on the

explanatory power of each variable one by one. Again, we used negative binomial regressions and for each adjusted model, the interest is to look at the direction of the interaction and whether the adjusted parameter is significantly different from zero. Each model has the following form:

$$\text{Log (dependant variable)} \sim a (\text{explanatory variable}) + b.$$

As we do 16 repeated models for each dependent variable, we took a significance level according to Bonferroni correction for multiple testing:  $\alpha = 0.05/16 = 0.003125$ . All manipulations of data and analyses were conducted with R software (R Core Development Team, 2015). Negative binomial regressions were conducted using the MASS package (Venables & Ripley, 2002).

## Results

### Monthly analysis

Strong relationships, structured in time and space, were observed both for the autocorrelation and rainfall (Table 1). Strong positive autocorrelations on the variable of total number of desert locust's reports in a given month ( $Y$ ) were observed at the 11 stations of the Algerian Sahara. These were significant autocorrelations with a lag of 1 month ( $Y_{-1}$ ), considering the surveys from a few tens of kilometres up to all the surveys in a 500 km radius for the stations in northern Algeria (from Bechar to In Salah). The most south-eastern stations had, in addition, an autocorrelation with a lag of 2 months (Illizi and Djanet), which implied a more sustained population dynamics in time. The stations in the far south of Algeria (Assekrem to In Guezzam) had a strong autocorrelation with 1 and 3 months lags, implying transgenerational population dynamics in these environments. Generation time is 2–3 months in favourable conditions, so if reports of locusts in a given month can be explained by locust presence 3 months earlier, this implies local dynamics with successive generations. If we considered only the larvae, in case of solitarious larvae populations (Table 2), positive autocorrelation was observed from north to south – as for the whole population –, but was also distributed more widely over time, and was observed for  $Y_{-1}$  (from north to south), for  $Y_{-2}$  (only in the north at Bechar and Adrar), and for  $Y_{-3}$  (in the south, roughly from Illizi to In Guezzam). For the transiens larvae (Table 3), positive autocorrelation was also observed from north to south, but solely and strictly for  $Y_{-1}$ .

The four stations south of the Sahara (In Guezzam, Bordj Badji Mokhtar, Tamanrasset, and Assekrem) showed a negative effect of total monthly rainfall on total number of observations for the same month (Table 1).



**Table 1** Monthly analyses by meteorological station (from north to south). It indicates the distances at which significant relationships were observed (numerical values of distances in km, and + or -, indicating a positive or negative relationship, respectively) between all the solitarious or transiens reports of desert locusts around each station (Y) and potentially explanatory variables: Y shifted by 1 ( $Y_{-1}$ ), 2 ( $Y_{-2}$ ), or 3 ( $Y_{-3}$ ) months, and P (rainfall) shifted by 1 ( $P_{-1}$ ), 2 ( $P_{-2}$ ), or 3 ( $P_{-3}$ ) months

Weather station	$Y_{-1}$	$Y_{-2}$	$Y_{-3}$	P	$P_{-1}$	$P_{-2}$	$P_{-3}$
Bechar	60–500: +		60–120: –	*	*340–500: –		
Timimoune	*80–500: +				*150–500: –	*	
Adrar	40–500: +				60–500: –		*
Tindouf	80–500: +				*160–500: –		100–500: +
In Salah	*140–500: +				*150–430: –		*
Illizi	*150–500: +	40–500: +					160–450: +
Djanet	80–500: +	*200–500: +					270–500: +
Assekrem	120–500: +	*	240–500: +	140–500: –		*	130–500: +
Tamanrasset	150–500: +	*	*120–500: +	120–500: –		*	*110–500: +
Bordj Badji Mokhtar	*280–500: +		350–500: +	410–500: –	*		*20–500: +
In Guezzam	*220–450: +		420–500: +	400–500: –		*	40–500: +

\*Relationships over less than three consecutive tens of kilometres were ignored to simplify interpretations.

**Table 2** Monthly analyses by meteorological station (from north to south) for solitarious desert locust larvae only. See Table 1 for explanation of variables and symbols used

Weather station	$Y_{-1}$	$Y_{-2}$	$Y_{-3}$	P	$P_{-1}$	$P_{-2}$	$P_{-3}$
Bechar	*50–90, 290–500: +	*200–500: +		*200–230: –, 430–500: +			
Timimoune	300–500: +		*	120–170: +		*	
Adrar	370–500: +	80–120: +	90–240: +	*		*	
Tindouf							
In Salah	*260–500: +			170–250: –	*		*
Illizi	*40–140, 420–500: +		430–500: +	*40–140: –			*
Djanet	370–500: +		400–500: +	330–350: –	*120–280: +	330–350: +	
Assekrem	120–500: +	*210–270, 350–500: –	*150–500: +	*210–270, 350–500: –	*	80–500: +	*
Tamanrasset	160–500: +	*300–500: –	*140–500: +	*300–500: –	*	110–500: +	*
Bordj Badji Mokhtar	390–500: +			*440–500: –		390–500: +	
In Guezzam	*440–500: +		410–500: +	440–500: –	330–440: +	*300–500: +	*170–200: +

\*Relationships over less than three consecutive tens of kilometres were ignored to simplify interpretations.

This was not observed for the northern and eastern stations. However, with a lag of 1 month, negative effects were observed for the northern stations (In Salah, Tindouf, Adrar, Timimoune, and Béchar). Finally, with a 3-month lag, the effects of rain were found to be positive for a majority of the stations (In Guezzam, Bordj Badji Mokhtar, Tamanrasset, Assekrem, Djanet, Illizi, and Tindouf) and generally started over 100 km from the station. Thus, the results were highly structured temporally and geographically. Considering solitarious nymphs only (Table 2), the geographic and temporal structure of relationships remained, even if modified compared to the whole population. We also found a negative effect of the

rain of the current month (P) for all the southern stations, from In Salah to In Guezzam. Positive effects (always at great distances from the weather station, usually >100 km) were observed earlier than for the overall population. They were observed with 1 or 2 months in advance, which seems logical given the larval development time ranging from 32 to 163 days depending on the season in Algeria (Symmons & Cressman, 2001). These positive relationships with P were observed in the north, in Bechar and Timimoune, and with  $P_{-1}$  and especially  $P_{-2}$  in the south, from Djanet to In Guezzam. For this last station of the extreme south a positive relationship was also noted at  $P_{-3}$ . For transiens larvae (Table 3), the spatial and

**Table 3** Monthly analyses by meteorological station (from north to south) for transiens desert locust larvae only. See Table 1 for explanation of variables and symbols used

Weather station	Y <sub>-1</sub>	Y <sub>-2</sub>	Y <sub>-3</sub>	P	P <sub>-1</sub>	P <sub>-2</sub>	P <sub>-3</sub>
Bechar	*110–500: +	*				*70–120: +	
Timimoune	*280–500: +	*			*	*	*
Adrar	*250–500: +			*	*370–500: –	*	
Tindouf	370–500: +			*370–490: +			
In Salah	140–500: +	*		*	210–330: –		*
Illizi	*			100–230: –		100–230: –	
Djanet	*						
Assekrem	*130–330: +				*100–290: +	*270–330: +	*250–290: +
Tamanrasset	*130–340: +				*130–350: +	*310–340: +	*
Bordj Badji Mokhtar	*						
In Guezzam	*300–500: +			360–450: +	*		310–430: +

\*Relationships over less than three consecutive tens of kilometres were ignored to simplify interpretations.

temporal structure almost disappeared. Positive relationships were observed from P to P<sub>-3</sub>, distributed from north to south. The majority of these relationships were in the south, mainly in Assekrem and Tamanrasset areas. Negative relationships were also observed from P to P<sub>-2</sub>. Overall, for transiens, geographic structure and temporal distribution of these relationships were not as clear as for solitary locusts.

Ultimately, these monthly analyses clearly show three large areas of different population dynamics in Algeria during recession periods: (1) northern and western Sahara (In Salah, Tindouf, Adrar, Timimoune, and Béchar), where the population dynamics of the desert locust occurs as temporal bursts, unpredictable locally; (2) southeast (Illizi and Djanet), where dynamics have a longer period, but also in response to local rainfall (3 months after the rains); and (3) south (In Guezzam, Bordj Badji Mokhtar, Tamanrasset, and Assekrem), where habitats can host several generations in the same year (autocorrelation to 3 months) and in response to local rainfall (3 months after the rains).

#### Annual analysis

For the three selected regions (Tamanrasset, Djanet, and Adrar), the number of reports of solitary locusts could be explained by the local presence of green vegetation (TV, DV, AV; Table 4). In addition, the reports of solitary locusts in the Adrar and Djanet regions (ANS, DNS) were significantly linked, and they were significantly related with the observations of transiens in Adrar (ANT). With a lower level of significance (significant at  $\alpha = 0.05$ , but not at  $\alpha = 0.003125$ , after Bonferroni correction), the number of solitary reports in Tamanrasset (TNS) could be explained by the number of transiens reports in the same

**Table 4** Results of annual analyses by region. Analyses were independent negative binomial regressions to explain number of reports of solitary or transiens desert locusts in a 200 km radius around the weather station of each region. The variable names are coded: the first letter indicates the region (T, Tamanrasset; D, Djanet; A, Adrar), 'N' the number of reports of solitary (NS) and transiens (NT) locusts, 'V' the proportion of green and greening vegetation in surveys, 'MP' the number of months with rain within the year, and '-1' indicates that the variable is shifted 1 year back to analyse temporal effects

Region	Reports in a 200 km radius	Significant explanatory variables (P value)*
Tamanrasset	Solitary, TNS	TV (2.5e-11), DNS (0.02), TNT (0.037)
Djanet	Transiens, TNT Solitary, DNS	TMP (0.0032) ANS (0.002), ANT (0.002), DV (1e-21), TNS (0.01), ANS <sub>-1</sub> (0.002)
Adrar	Transiens, DNT Solitary, ANS	DNS-1 (0.01), DV (1e-24) DNS (0.0007), ANT (0.0003), AV (8e-6)
	Transiens, ANT	–

\*After Bonferroni correction,  $P < 0.003125$  indicate significant effects.

region (TNT) and by the number of solitary reports in Djanet (DNS). Similarly, the number of solitary in Djanet (DNS) could be explained by the number of solitary in Tamanrasset (TNS) and by the number of solitary in Adrar during the previous year (ANS<sub>-1</sub>). All these relationships pointed out interdependence between regions, and these joined dynamics were likely the result of exchanges between populations.

For the number of transiens reports it was more difficult to find a general explanation. For Djanet, transiens reports could be explained by the local presence of green vegetation (DV), and to a lesser degree by the number of solitarious reports of the previous year in the same region (DNS-1), implying possible local interannual dynamics, although this does not exclude links with other regions. In Tamanrasset, transiens reports were linked only with the total number of rainy months of the current year (TMP), reinforcing the suspicion that gregarization can take place in this region. Finally, transiens reports in Adrar were not significantly related to any variable. Overall, no autocorrelation was found, and annual rainfall level (P) and the level of global invasion (I) were not retained as explanatory variable in any of the three regions, regardless of the phase, solitarious, or transiens.

## Discussion

The analysis of data archives about desert locust in Algeria provides interesting lessons on environmental factors influencing the development of locust populations and their dynamics in this country. We observed a clear difference between the northern and southern Saharan regions of Algeria concerning locust dynamics and the impact of environmental conditions. A link between green vegetation and presence of solitarious locusts could be observed on an annual basis. In addition, relationships between various locations demonstrated clear regional dynamics. We discuss how these findings confirm the importance of runoff and of migrations of solitarious populations, and their implications on operational purposes.

### North and south differences in light of water availability

Water availability is considered as the main limiting factor for the development of locusts in the Saharan zone (Duranton & Lecoq, 1990; Ould Elhadj, 2002). At the monthly level, the spatially and temporally structured relationships between accumulated rainfall and locust reports confirmed the importance of rainfall for the development of locust populations. However, at the yearly time scale, the rainfall variable is not explanatory in any of the three regions and regardless of the phase status, solitarious, or transiens. Only for Tamanrasset, the weak relationship between number of rainy months and transiens observations per year might be explained by the potential of this area to host gregarization processes (Popov, 1997; Lecoq, 2001, 2012). Other relationships between rainfall and locust reports at the yearly level are not significant. This is contrary to the common belief that wet years are favourable for locusts.

The characteristic delayed positive relationships between monthly rainfall and locust observations in the southernmost stations (Illizi, Djanet, In Guezzam, Bordj Badji Mokhtar, Tamanrasset, and Assekrem) are probably due to slow runoff (on surface or underground) from Saharan mountains (Hoggar, Tassili n'Ajjer, Adrar des Iforas) in these areas. We can estimate that 3 months is about the time required between a rain event and the water runoff to potentially favourable areas for locusts (according to their soil and botanical characteristics), the gathering and breeding of parental locusts, the appearance of green vegetation, and the development of a first autochthonous generation of locusts (Duranton & Lecoq, 1990). The negative effects during the first months in these southernmost areas are probably the result of the difficulty to access the areas where the rainfalls or has just fallen.

In the case of solitarious larvae the interpretation is probably similar. Simply, the time to observe a positive relationship after rain is shorter and goes to 2 months for the southernmost stations. Hence, the time needed for autochthonous populations to reach the hopper stages is shorter than when looking at the global population (larvae and adults). For transiens larvae, there is no clear temporal or spatial structuring of the relationships. All relationships seem distributed randomly. One might conclude that when the gregarization process is engaged, the rain is not the best indicator of the presence of larvae. This seems consistent with what is known otherwise of the gregarization process, which happens more likely in clumpy and drying habitats (Bouaïchi et al., 1996; Despland et al., 2000; Cisse et al., 2013, 2015). This is also consistent with the less strict ecological requirements of transiens and gregarious – compared to solitarious – desert locusts (Despland, 2005).

For the habitats of the northern Sahara (Béchar, Timimoun, Adrar, and In Salah areas), no strong positive effect of the rain was observed on the locust records. This could be explained by the limiting effect of temperature, often too low in winter, on locust development in these areas. We know that in these more northern regions of the Sahara, the desert locust populations spend most of the winter in adult quiescence, and that the reproduction period begins in the spring, with temperature rising (Waloff, 1976; Popov et al., 1991; Popov, 1997). The rains falling from late fall to early spring then remain without significant impact. For example in Bechar, despite significant rains between November and February (8–15 mm per month, on average), low temperatures (<15 °C average monthly air temperature) are incompatible with the reproduction of the desert locust. Further studies considering climate change should be conducted to evaluate whether these areas might become more favourable to desert locust in the future.



Our results stressed that rain effects were visible over considerable distances from the rainfall area. This is certainly the impact of water runoff in the many wadis flowing from the Saharan mountains. These results are in agreement with various other studies that have shown that the desert locust activity in the central Sahara is mostly linked to runoff coming from the Saharan mountains but not directly to rainfall (Dubief, 1963; Popov, 1965, 1997; Sitouh, 1976). Potential areas of desert locust breeding in these regions are largely fed by runoff caused by rainfall on the massifs of Hoggar, Tassili n'Ajjer, Adrar, or Atlas. These rains are relatively abundant on the mountains compared to the quantities recorded at lower elevations. The annual average of the Assekrem station located in the Hoggar massif is around 123 mm. At lower altitude, Tamanrasset and Adrar will receive, on average, 51 and 16 mm of rain, respectively. Since some years, another source of water is constituted by the irrigation of large farms in the central Sahara (Adrar and In Salah). This irrigation comes in substitution of rains and runoff. These areas may enable the desert locust to find favourable ecological conditions for its development for several consecutive months (Ould Elhadj, 2002; Guendouz-Benrima et al., 2007) and hence reduce the importance of rainfall as explanatory variable of locust presence.

#### Vegetation effects

Concerning the records of green vegetation in the locust database, their use must be balanced by a biased statistical construction: observations of the vegetation take place only when the survey teams are in the field looking for locusts. Thus, at a monthly level, these variables are structurally correlated and do not necessarily inform about relationships between vegetation and development of locust populations – by the way, such relationships are well-known (e.g., Popov et al., 1991). Through our analysis on an annual basis, the bias decreases because surveys may continue for several months after population development. We observed a strong relationship between observations of solitary locusts and the presence of green vegetation on an annual basis. It is known that locusts only develop favourably in a green vegetation able to support larval development and that of the young imagos (Popov et al., 1991; Popov, 1997). Such a relationship is also well established at a finer time scale (e.g., Piou et al., 2013). In general, in the Saharan environment, favourable conditions only persist for a short period of time. After the soil dries out as well as the vegetation, locusts will remain in reproductive quiescence, flying around, looking for a new wet and green habitat. This nomadic strategy allows them to better survive in these hyper-arid environments (Duranton & Lecoq, 1990). It explains that the adult

locusts could be found, a good part of the year, in dry environments, but concentrate in the areas of green vegetation. Occasionally, populations may persist for many months in the same place thanks to persistent suitable conditions of turgid and green vegetation (Popov, 1997). This favourable green vegetation naturally results from a soil wetting (by rain, runoff, or capillary rise of shallow waters) which means that the rain cannot be effectively correlated with locust populations. As we currently lack information on soil moisture, only the green vegetation is a good indicator of a successful development and of potential presence of locusts. Piou et al. (2013), through the use of various indicators extracted from satellite imagery, have also shown that the development of the vegetation is among the best predictors of the presence of locusts.

In these desert areas, the development time of vegetation varies greatly among species. For example, the cycle of the two annual plant species most appreciated by the desert locust is between 6 weeks for *Tribulus mollis* Ehrenb. ex Schweinf. and 5 months for *S. purpurea* (Popov, 1997). Depending on the type of habitat where rainwater falls or trickles, the persistence of favourable conditions for locusts is very variable. This variability makes it more difficult to generalize a vegetation–locust relationship on extended spatial and temporal scales. Nevertheless, this relationship was clearly demonstrated in our study of the solitary locusts. However, it was almost absent for transients, except in the region of Djanet, and it is probably non-existent for gregarious locusts that exhibit much less stringent ecological preferences and occur in more diverse habitats (Despland, 2005). Thus, our study clearly illustrates the value of targeting surveillance on solitary locusts, the only phase for which a locust–vegetation relationship is clearly established.

#### Local and regional dynamics

Our results also suggest an impact of local and regional dynamics on the development of desert locust, with high temporal autocorrelation. At a monthly scale, the strong autocorrelation at 1 month for all stations is quite trivial. Indeed, a locust generation lasts at least 2–3 months in favourable conditions and the presence of locusts in a given month (especially in case of the presence of larvae) implies some probability of also having a locust presence the following month. However, we observed this autocorrelation over great distances from each station, often up to 500 km. This suggests that environmental conditions favourable to locust development occur frequently over large areas, probably also as a result of runoff. Moreover, this relationship extends in time towards the south. It extends over 2 months at Illizi and Djanet, and 3 months for all the stations further south. This implies a more

sustained population dynamics in southern Algeria than in the north. For the four southernmost stations this even demonstrates the non-negligible probability of having two successive generations.

The positive autocorrelations over several months in the north may reflect the existence of a single generation due to lower temperatures and thus a longer development time. In the case of transiens larvae, where autocorrelation is observed only at a lag of 1 month, our results may imply a dynamics with a single transiens generation. The previous generations might have been either solitarious or in other areas. Moreover, the following generations are either inexistent on site due to control and/or migration or would likely be considered as gregarious and hence excluded from our analyses.

These results are consistent with the view of the dynamics of the desert locust in Algeria, knowledge that is mostly based on invasion periods (Waloff, 1966, 1976; Pedgley, 1981). In the north of Algeria a single generation takes place during spring (March–May, when temperatures are sufficient) due to the winter and spring rains. With the drying of the vegetation, adults will migrate southwards to take advantage of the monsoon rains. In the south, the desert locust reproduces in summer (June to August). The monsoon rains might allow the development of a single generation, but two successive generations may also occur when the rainy season is long enough. This second generation occurs in autumn, from August to November approximately (Sitouh, 1976), under favourable thermal conditions. Our study confirms that these dynamics appear to be identical in recession period.

At the annual level, the dynamics of solitarious locusts (and, more weakly, of transiens) can be partly explained by the locust situation in other regions. This highlights a certain level of population exchanges between these areas. We know that solitarious desert locusts move seasonally, at night, in search for suitable breeding conditions (Symmons & Cressman, 2001; Roffey & Magor, 2003). Thus, the existence of complementary seasonal breeding areas is an important feature in the population dynamics of this species and its survival strategy in the desert (Uvarov, 1977). Such relationships between different regions are probably more general than suggested by the few annual correlations observed here. The absence of autocorrelation on an annual basis indicates that these solitarious populations migrate seasonally from one country to another. As a result, populations returning to Algeria may have little connection with those that left the country a few months earlier. Migration of solitarious populations is supported by population genetic studies. Chapuis et al. (2014) demonstrated that populations of solitarious locusts have no appreciable genetic structure in their entire distribution

range, from Mauritania to Pakistan. This indicates regular mixing between solitarious populations and significant dispersal ability. However, such movements do not exclude local interannual dynamics as found for Djanet, i.e., a relationship between transiens locusts of 1 year and solitarious locusts of the previous year in the same region.

We observed temporal autocorrelation at the monthly level for transiens and solitarious individuals, as Tratalos et al. (2010) found for gregarious swarms. However, the autocorrelation was not discernible at the year level and no transiens–transiens link between regions was observed (and few solitarious–transiens links). This is surely related to the need of complementary reproduction areas throughout a year across several countries and the migrations of locusts among these countries. This emphasizes that international collaboration is essential at the national management level.

#### Operational implications

From an operational point of view, our results can help the locust control service of Algeria to improve its preventive management by better targeting the areas to be monitored, especially in the early stages of gregarization (Magor et al., 2008; Sword et al., 2010). The aim is to limit the excessive use of insecticides and reduce the high costs of locust survey and control campaigns. The complexity of the relationship between locusts and environmental factors reinforces the argument for a flexible and scalable preventive system. A clear difference between the northern and southern Saharan areas of Algeria may require rethinking the organization of prevention. Heavy rains in the south are correlated with locust outbreaks and ask for strengthening survey operations, whereas in the north routine surveys in winter could suffice. National planning of locust monitoring should also take into account the international situation in case migratory groups are formed elsewhere. As the transiens phase marks the first stages of gregarization and possible progressive development to invasion, a precise characterization of the transiens populations – using better behaviour, pigmentation, and morphology (desert locust: Duranton & Lecoq, 1990; red locust: Lecoq et al., 2011) – is crucial for effective prevention. In addition, the comprehensive mapping of wadis, and their integration into a geographic information system, could significantly improve the efficiency of the monitoring system (Lazar et al. 2015). Measuring soil moisture with satellites is still difficult (but see Merlin et al., 2013), but monitoring green vegetation is a good alternative (Piou et al., 2013). As the relationship between desert locust and soil moisture (rain or runoff) is perceived clearly for solitarious hoppers and not – or less clearly – for transiens hoppers,

the focus of surveys should be on the solitary phase for quick location of any gathering population which may become transients and hence be potentially dangerous. Waiting for gregarious populations to occur, as advocated by some (Symmons, 2009), ignores the increasingly effective and precise detection capabilities offered by modern satellite imagery. These techniques would be less useful for gregarious populations. Monitoring and survey of solitary locust populations must be reinforced whenever possible.

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### References

- Akaike H (1973) Information theory and an extension of the maximum likelihood principle. Second International Symposium on Information Theory (ed. by BN Petrov & F Csaki), pp. 267–281. Akadémiai Kiadó, Budapest, Hungary.
- Babah Ebbe MA (2008) Biogéographie du Criquet Pèlerin (*Schistocerca gregaria*, Forskål, 1775): Identification, Caractérisation et Originalité d'un Foyer Grégarigène en Mauritanie Centrale. PhD Dissertation, Ecole Pratique des Hautes Etudes, Paris, France.
- Bouaïchi A, Simpson SJ & Roessingh P (1996) The influence of environmental microstructure on the behavioural phase state and distribution of the Desert locust *Schistocerca gregaria*. *Physiological Entomology* 21: 247–256.
- Brader L, Djibo H, Faye FG, Ghaout S, Lazar M et al. (2006) Towards a More Effective Response to Desert Locusts and their Impacts on Food Insecurity, Livelihoods and Poverty. Multilateral Evaluation of the 2003-05 Desert Locust Campaign. FAO, Rome, Italy.
- Chapuis MP, Plantamp C, Blondin L, Pagès C & Lecoq M (2014) Demographic processes shaping genetic variation of the solitary phase of the Desert locust. *Molecular Ecology* 23: 1749–1763.
- Chapuis MP, Plantamp C, Streiff R, Blondin L & Piou C (2015) Microsatellite evolutionary rate and pattern in *Schistocerca gregaria* inferred from direct observation of germline mutations. *Molecular Ecology* 24: 6107–6119.
- Cisse S, Ghaout S, Mazih A, Babah Ebbe MAO, Benahi AS & Piou C (2013) Effect of vegetation on density thresholds of adult desert locust gregarization from survey data in Mauritania. *Entomologia Experimentalis et Applicata* 149: 159–165.
- Cisse S, Ghaout S, Mazih A, Ould Babah Ebbe MA & Piou C, (2015) Estimation of density threshold of gregarization of desert locust hoppers from field sampling in Mauritania. *Entomologia Experimentalis et Applicata* 156: 136–148.
- Cressman K (2001) Desert Locust Guidelines. 2. Survey. FAO, Rome, Italy.
- Cressman K & Hodson D (2009) Surveillance, information sharing and early warning systems for transboundary plant pests diseases: the FAO experience. *Arab Journal of Plant Protection* 27: 226–232.
- De Vreyer P, Guilbert N & Mesple-Sompsa S (2014) Impact of natural disasters on education outcomes: evidence from the 1987–89 locust plague in Mali. *Journal of African Economies* 24: 57–100.
- Despland E (2005) Diet breadth and anti-predator strategies in Desert locusts and other Orthoptera. *Journal of Orthoptera Research* 14: 227–233.
- Despland E, Collett M & Simpson SJ (2000) Small-scale processes in Desert locust swarm formation: vegetation patterns influence gregarization. *Oikos* 88: 652–662.
- Dubief J (1963) Le Climat du Sahara. Institut de Recherches Sahariennes, Université d'Alger, Alger, Algeria.
- Duranton J-F & Lecoq M (1990) Le Criquet pèlerin au Sahel. Collection Acridologie Opérationnelle no. 6. Comité Inter-Etats de Lutte contre la Sécheresse dans le Sahel. Département de Formation en Protection des Végétaux, Niamey, Niger.
- Duranton J-F, Foucart A & Gay PE (2012) Florule des Biotopes du Criquet Pèlerin. CIRAD, Montpellier, France.
- FAO (1968) Desert Locust Project, Final Report. FAO/SF: 34/DLC, FAO, Rome, Italy.
- FAO (1972) Projet Relatif au Criquet Pèlerin, Rapport Complémentaire (Juillet 1966-Décembre 1970). FAO/SF: 34/DLC. FAO, Rome, Italy.
- Guendouz-Benrima A, Duranton J-F, El Habib Benhammouda M & Doumandji Mitiche B (2007) Distribution des populations de Criquet pèlerin *Schistocerca gregaria* Forsk 1775 (Insecta, Orthoptera) en période de rémission en Algérie de 1983 à 2000. *Science et Changements Planétaires/Sécheresse* 18: 246–253.
- Hafraoui A & McCulloch L (1993) Present practices of controlling Desert locust outbreaks. Atelier International de la FAO sur la Recherche et la Planification en Matière de Lutte Contre le Criquet Pèlerin Tenu à Marrakech (Maroc) du 24 au 28 Mai 1993. FAO, Rome, Italy.
- van Huis A (2007) Locust control by early identification of breeding sites. *Encyclopedia of Pest Management* 240: 1–3.
- van Huis A, Cressman K & Magor JI (2007) Preventing desert locust plagues: optimizing management interventions. *Entomologia Experimentalis et Applicata* 122: 191–214.

- Joffe S (1995) Desert Locust Management: A Time for Change. World Bank Discussion Paper 284, The World Bank, Washington, DC, USA.
- Krall S, Peveling R & Ba Diallo D (1997) New Strategies in Locust Control. Birkhäuser, Basel, Switzerland.
- Lazar M, Diongue A, Yang J-T, Doumandji-Mitiche B & Lecoq M (2015) Location and characterization of breeding sites of solitary Desert locust using satellite images Landsat 7ETM+ and Terra MODIS. *Advances in Entomology* 3: 6–15.
- Lecoq M (1975) Les Déplacements par Vol du Criquet Migrateur Malgache en Phase Solitaire: Leur Importance sur la Dynamique des Populations et la Grégorisation. Ministère de la Coopération, Paris, France.
- Lecoq M (1978) Biologie et dynamique d'un peuplement acridien de zone soudanienne en Afrique de l'Ouest (Orthoptera, Acrididae). *Annales de la Société Entomologique de France* 14: 603–681.
- Lecoq M (2001) Recent progress in desert and migratory locust management in Africa. Are preventative actions possible? *Journal of Orthoptera Research* 10: 277–291.
- Lecoq M (2003) Desert locust threat to agricultural development and food security and FAO/International role in its control. *Arab Journal of Plant Protection* 21: 188–193.
- Lecoq M (2004) Vers une solution durable au problème du criquet pèlerin? *Science et Changements Planétaires/Sécheresse* 15: 217–224.
- Lecoq M (2005) Desert locust management: from ecology to anthropology. *Journal of Orthoptera Research* 14: 179–186.
- Lecoq M (2012) Bioécologie du Criquet Pèlerin. FAO-CLCPRO, Alger, Algeria.
- Lecoq M, Chamouine A & Luong-Skovmand MH (2011) Phase-dependent color polyphenism in field populations of red locust nymphs (*Nomadacris septemfasciata* Serv.) in Madagascar. *Psyche* 2011: 105352.
- Magor JI (1994) Desert locust population dynamics. Desert Locust Control with Existing Techniques: An Evaluation of Strategies. Proceedings of the Seminar Held in Wageningen, The Netherlands, 6–11 December 1993 (ed. by A van Huis), pp. 31–54. Agricultural University, Wageningen, The Netherlands.
- Magor JI, Ceccato P, Dobson HM, Pender J & Ritchie L (2007) Preparedness to Prevent Desert Locust Plagues in the Central Region: An Historical Review. Desert locust Technical Series 35. FAO, Rome, Italy.
- Magor JI, Lecoq M & Hunter D (2008) Preventive control and Desert locust plagues. *Crop Protection* 27: 1527–1533.
- Matthews RW & Matthews JR (2009) *Insect Behavior*, 2nd edn. Springer, New York, NY, USA.
- Merlin O, Escorihuela MJ, Mayoral MA, Hagolle O, Al Bitar A & Kerr Y (2013) Self-calibrated evaporation-based disaggregation of SMOS soil moisture: an evaluation study at 3 km and 100 m resolution in Catalunya, Spain. *Remote Sensing of Environment* 130: 25–38.
- Ould Elhadj MD (2002) Les nouvelles formes de mise en valeur dans le Sahara algérien et le problème acridien. *Science et Changements Planétaires/Sécheresse* 13: 37–42.
- Pasquier R (1942) Les sauterelles pèlerines. L'invasion actuelle, les recherches, la lutte. *L'Agria* 99: 1–12.
- Pedgley DE (1981) Desert Locust Forecasting Manual. Centre for Overseas Pest Research, London, UK.
- Pener MP (1991) Locust phase polymorphism and its endocrine relations. *Advances in Insect Physiology* 23: 1–79.
- Pener MP & Simpson SJ (2009) Locust phase polyphenism: an update. *Advances in Insect Physiology* 36: 1–272.
- Piou C, Lebourgeois V, Sidi Benahi AS, Bonnal V, El Hacen Jaavar M et al. (2013) Coupling historical prospection data and a remote-sensing vegetation index for the preventative control of Desert locust. *Basic and Applied Ecology* 14: 593–604.
- Popov GB (1965) Review of the Work of the Desert Locust Ecological Survey June 1958–March 1964 and the Considerations and Conclusions Arising From It. Report no. UNSF/DL/ES/8, FAO, Rome, Italy.
- Popov GB (1997) Atlas of Desert Locust Breeding Habitats. FAO, Rome, Italy.
- Popov GB, Duranton J-F & Gigault J (1991) Etude Écologique des Biotopes du Criquet Pèlerin *Schistocerca gregaria* (Forskål, 1775) en Afrique Nord-Occidentale: Mise en Évidence et Description des Unités Territoriales Écologiquement Homogènes. Collection les Acridiens, CIRAD-PRIFAS, Montpellier, France.
- R Core Development Team (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rainey RC (1963) Meteorology and the migration of Desert locust. Applications of synoptic meteorology in locust control. *Anti-Locust Memoir* 7: 1–115.
- Rainey RC (1971) Some implications of the present status of Desert locust (*Schistocerca gregaria* Forsk.). 13th International Congress of Entomology, 2–9 August 1968, Moscow. USSR, Abstract Volume 2: 379.
- Roffey J & Magor JI (2003) Desert Locust Population Parameters. FAO, Rome, Italy.
- Sitouh M (1976) Relations entre les crues et *Schistocerca gregaria* Forsk. en phase solitaire dans le Sahara central de 1967 et 1972. *Annales de l'Institut National Agronomique* 4: 33–83.
- Sword GA (2008) Gregarious behaviour in insects. *Encyclopedia of Entomology* (ed. by J Capinera), pp. 1733–1740. Springer, Dordrecht, The Netherlands.
- Sword GA, Lecoq M & Simpson SJ (2010) Phase polyphenism and preventative locust management. *Journal of Insect Physiology* 56: 949–957.
- Symmons P (2009) A critique of 'Preventive control and Desert locust plague'. *Crop Protection* 28: 905–907.
- Symmons P & Cressman K (2001) Desert Locust Guidelines. 1. Biology and Behaviour. FAO, Rome, Italy.
- Tratalos JA, Cheke RA, Healey RG & Stenseth NC (2010) Desert locust populations, rainfall and climate change: insights from phenomenological models using gridded monthly data. *Climate Research* 43: 229–239.
- Uvarov BP (1977) Grasshoppers and Locusts. A Handbook of General Acridology. II: Behaviour, Ecology, Biogeography,

- Population Dynamics. Centre for Overseas Pest Research, London, UK.
- Venables WN & Ripley BD (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York, NY, USA.
- Waloff Z (1966) The upsurges and recessions of the Desert locust plague: an historical survey. *Anti-Locust Memoirs* 8: 1–111.
- Waloff Z (1976) Some temporal characteristics of Desert locust plagues. *Anti-Locust Memoirs* 13: 1–36.