

Quantitative analysis of behavioural phase difference in *Locusta migratoria migratorioides* (Reiche & Fairmaire, 1849) (Orthoptera, Acrididae) from the examination of spatial distribution patterns

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Abstract

The field of animal behaviour has often relied on tracking and recording the behaviour of a single individual. For example, for decades, gregarious locust behaviour research has used a standard assay that tracks the path of an individual in a cell, including how much time it spends next to an adjacent cell containing a group of stimulus locusts. However, this process can be time-consuming and impractical in lab and field settings. Here, we validate a complementary approach that uses spatial distribution patterns of a group of locusts in a circular arena to characterize the level of gregarious behaviour. We examined temporal variations in nearest neighbour distances as a criterion of attraction–repulsion and the successive changes of position of the individuals as a criterion of activity level. We used 3rd instar juveniles of the Migratory Locust, *Locusta migratoria migratorioides* (Reiche and Fairmaire 1849), reared in isolated or crowded conditions. Locusts exhibit density-dependent plasticity, and crowd-rearing induces gregarious behaviour. As predicted, we found a larger nearest-neighbour distance between isolated-reared hoppers (indicating repulsion) than mass reared hoppers, which showed attraction to their conspecifics. Mass reared locusts walked greater distances, marking higher activity levels, which is another characteristic of gregarious locusts. These results indicate that this is an efficient and effective method of quantifying gregarious behaviour.

Keywords: *Locusta migratoria migratoria*; Phase polyphenism; Attraction; Repulsion · Activity; Video tracking; Orthoptera, Acrididae

Introduction

The behavioural phase of the Migratory Locust, *Locusta migratoria migratorioides* (Reiche and Fairmaire 1849), has been intensively studied and has always fascinated researchers across generations since the understanding of the phase change process (Zolotarevskby 1930; Uvarov 1966; Pener 1991). The behaviour is the first noticeable feature of phase change and hence is of utmost importance in understanding the complex relationships between individuals and their environment (Simpson et al. 1999) to develop efficient management strategies. Other phase features, such as changes in body colour or morphometric and physiologic traits, gradually occur through generations of overcrowding (Uvarov 1977; Simpson et al. 2005). Hence, the plasticity of this species with the related underlying mechanisms causing cohesive migrations has been a central topic for quite a long time. Like other locusts around the world, the Migratory Locust exhibits phenotypic plasticity in response to local density (Chapuis et al. 2009). In addition to density, other factors could cause rapid maturation and breeding, leading to a shorter lifecycle inducing phase change from grouping in restricted areas (Launois and Launois-Loung 1998; Allal-Benfekih 2006). These factors include seasonal variations in rainfall, photoperiod, temperature and carbon dioxide content, scarcity of favourable habitats, quality of nutrition and soil salinity (Grassé 1949; Appert and Deuse 1982; Rainey 1989). The Migratory Locust is the most widespread and usually lives isolated at low density in solitarious form. When weather conditions facilitate several successful generations of breeding, individuals at high density congregate and change progressively to the gregarious form, these gregarious individuals are well known for their capacity to form gigantic and devastating bands of wingless hoppers, which later become swarms of winged adults. Gregarious and solitarious forms are morphologically, anatomically, physiologically, and behaviorally different (Uvarov 1966, 1977; Randriamanantsoa 1998; Pener 1991). Solitarious migratory locusts are green or brown according to the seasonal moisture environment (the green forms are predominant in the wet season and the brown forms in the dry season), avoid other locusts and do not cause problems, while gregarious locusts are orange or yellow with black spots and aggregate with conspecifics (Farrow 1972, 1975, 1987; Uvarov 1977). Also, solitarious hoppers of the Migratory Locust are sedentary and spend most of the day basking on the ground or resting in the plants. On the contrary, the gregarious hoppers live in groups or bands and carry out a characteristic daytime wandering called marching band (Ellis 1953).

Several works have used different approaches to highlight attraction/avoidance to other locusts as measurements of phase behaviour. The first approach combines several ethological observations of the individual facing a group of stimuli in an arena to detect various activity-related phase behaviours (Islam et al. 1994; Bouaïchi et al. 1995; Tanaka and Nishide 2012). This approach, also tested with *Schistocerca gregaria* (Desert Locust), was very advantageous to simultaneously assess several behavioural parameters at the individual level (Roessingh and Simpson 1994; Simpson et al. 2001). This methodology allowed significant progress in understanding the physiological mechanism of the phase change process (Anstey et al. 2009). Despite deep acceptance (Rogers et al. 2014; Cullen et al. 2017), this method presents limitations as it does not allow either observing at the same time several individuals' behaviours or highlighting attraction-related behaviour at the spatial scale of distribution of individuals within a group (Sword 2003). Automated computer analyses were proposed to answer the limitation of single-individual analysis and permit simultaneously examining a

group of individuals (Gray et al. 2009; Cullen et al. 2012). Another approach, used since the 1950s, involves observing group-level behaviour through assessing activity and aggregation tendencies (Ellis 1953, 1959). This idea of observing several individuals simultaneously within the same arena was improved successfully with the help of spatial statistics to investigate the differences in behaviours of Desert locust in laboratory and field conditions (Cisse et al. 2015). Alternatively, several studies have used actographs to measure locomotion activity to characterize behavioural phase-related differences (Edney 1937; Harano et al. 2009, 2011). These actographs allow the simultaneous analysis of several individuals' behaviour and locomotion activity under different conditions such as diet or light intensity. They, however, cannot measure attraction-related behaviours.

Cisse et al. (2015) developed a diagnostic tool for characterizing the behavioural phase from the analysis of the spatial distribution pattern of individuals in a circular arena. To that end, orthogonal photo sequences taken at regular intervals were used to estimate the nearest neighbour distance (NND) variations between individuals in an arena to measure attraction/avoidance behaviour. The activity levels were approximated with the variations of the positions of individuals on successive photographs. First, this method allows an extended follow-up of the aggregation behaviour and activity levels of individuals, whatever their gregarious or solitary origin. Second, it allows a comparison of the individuals' spatial distribution with a random process. However, the disadvantage of this approach is that the events between two successive photographs taken at one-minute intervals were not recorded. The absence of continuous recording suggested that some movement and activity could be underestimated in the previous study (Cisse et al. 2015).

Another question that emerged from Cisse et al. (2015) study was the sequence of behaviour changes in the gregarization process. For *S. gregaria*, it seems that during the two hours of the experiments, the individuals would modify their activity more than their attraction levels.

In this context, the present work experiments a video tracking technique to allow a continuous and complete follow-up of the locusts in a circular arena to detect their activity status and attraction levels. The objectives are 1) to improve the phase characterization approach with point pattern analysis related to the attraction/avoidance behaviour and a measure of activity level in continuous time and 2) to check if the change in activity precedes the change in aggregation behaviour in the Migratory Locust during the first two hours of the gregarization process.

Materials and methods

Locust hoppers and rearing conditions

Hoppers of *Locusta migratoria* were issued from a mass breeding line for more than 10 generations. No phase change from gregarious to solitary occurred during the rearing of those 10 generations of gregarious locust, which were used for the validation analysis. At hatching time, two rearing conditions were used: 1) isolation in a plastic box (8 cm × 8 cm × 12 cm) and 2) group-reared hoppers in cages (about 40 to 80 hoppers in a cage of 24 cm × 19 cm × 19 cm). Each hopper was isolated in plastic box (8 cm × 8 cm × 12 cm) to induce the solitary behavior. On the other hand, 40 to 80 newly born larvae were placed in a

single cage to create overcrowding conditions for maintaining gregarious behavior. The experimental conditions in lab were good enough and there was no mortality in the boxes concerned.

These hoppers were kept in these conditions until the third instar to obtain distinct phase characteristics between "solitarious hoppers" and "gregarious hoppers" (Roessingh et al. 1993). The rearing chamber was set to $31 \pm 1^\circ \text{C}$ under a photoperiodic alternation (light/dark) of 12:12 h with a relative humidity of $50 \pm 10\%$. The hoppers were fed with new wheat shoots every two days. The influence of food on the process has not been studied. As we know, grasses are plants well appreciated by this type of locust; we simply used what can be easily produced in the laboratory. There is no cause and effect on this choice of wheat shoot. The meshes of the cover ensured the aeration of the boxes to avoid condensation and moisture excess, which can be generated by the food. The boxes were translucent, and a compressed air stream was continuously sent to the rearing room to avoid olfactory interactions between hoppers.

Behavioural arena and data collection

The behavioural arena was circular (Height = 40 cm and Diameter = 54 cm), made of a whitish Plexiglas sheet, and a thin layer of Insect-a-Slip covered the inner wall (Fluon BioQuip Products, Rancho Dominguez CA, USA) to prevent hoppers from climbing. A digital video camera (DFK 21AU04, The ImagingSource®) connected to a computer and positioned at 2 m height was installed above the arena to follow the movements of individuals (Fig. 1). Floodlighting and room heating were harmonized to avoid hot spots that may attract the hoppers. The tests included introducing 15 hoppers of the third hopper instar from group or isolation rearing into the behavioural arena. The hoppers were previously collected and placed in a small box (8 cm × 8 cm × 12 cm) for a short time (2 ± 1 min) to transport them to the test room. The tests lasted two hours. A total of six pairs of tests were conducted with hoppers reared in groups or isolation at the same age and on the same days.

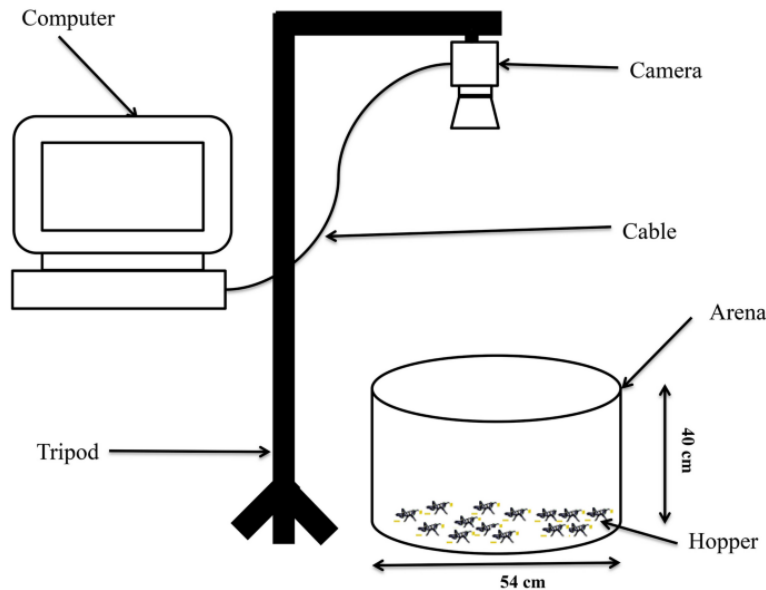


Fig. 1. Schematic of the experimental arrangement

Video acquisition and data processing

The video acquisition was conducted with the IC Capture software (v2.4 ImagingSource®) at 15 frames/seconds. The videos were processed using Ctrax version 0.5 (Branson et al. 2009) using "Dark flies on light background", ellipse shapes of "flies" to gather the individual hopper's position and orientation at each frame on the circular part of the video corresponding to the arena. This allowed the computation of the nearest neighbour distances (NND) between individuals. This is an indirect measurement of attraction/avoidance behaviour. As the individual identities of hoppers were registered and maintained over test time, we could estimate their activity level through the walked distance per period of 10 s.

Secondly, we did hand digitalization of some extracted images to verify the conclusions obtained from the analysis with Ctrax. For this, we extracted images from the video every 5 min using the FFmpeg software (<https://ffmpeg.org>). Hence, for each video, we obtained a sequence of 25 successive photographs describing the spatial and temporal variation of the position of each individual in the arena. As mentioned above, the computation of the NND values was an indicator of spatial relationships among individuals (aggregation or regularity, attraction, or repulsion).

Statistical analyses

Using student T-tests, we compared the mean values of NND and activity per 20 min periods between each experiment (isolated-reared or mass reared). We repeated these analyses for the NND estimated from the by-hand digitalization. Additionally, we compared the mean value of NND estimated by hand with the one estimated with Ctrax for each period and treatment. All analyses were run with the R software (R Core Team 2017).

Nearest neighbor analysis examines the distances between each hopper (point) and the closest hopper (point) to it, and then compares these to expected values for a random sample of points from a CSR (complete spatial randomness) pattern.

Formula

(a) The mean nearest neighbor distance

$$\bar{d} = \left(\sum_{i=1}^N d_i \right) / N \quad (1)$$

where N is the number of points. d_i is the nearest neighbor distance for point i.

(b) The expected value of the nearest neighbor distance in a random pattern

$$E(d_i) = 0.5 \sqrt{(A/N)} + \left(0.0514 + \frac{0.041}{\sqrt{N}} \right) * B / N \quad (2)$$

where A is the area and B is the length of the perimeter of the study area.

(c) The variance

$$Var(\bar{d}) = 0.070 A / N^2 + 0.037B \sqrt{(\sqrt{A} / N^2)} \quad (3)$$

Equations (2) and (3) contain a correction factor to account for the boundary effect based on Donnelly (1978).

Results

Nearest neighbor distances

With Ctrax digitalization, the mean nearest-neighbour inter-individual distances (meanNND) remained different between isolated-reared and mass reared throughout the experiments (Fig. 2). Independent of the time steps, mass reared hoppers showed a shorter mean NND (from 4.720 to 5.516 cm) than isolated reared (from 6.171 to 7.024 cm) (Table 1). The standard deviation remained relatively low (1.390–1.598 cm for isolated reared and 0.920–1.534 cm for mass reared). Overall, the median NND of mass reared hoppers was 5.161 cm, while the median NND of isolated-reared hoppers was 6.677 cm.

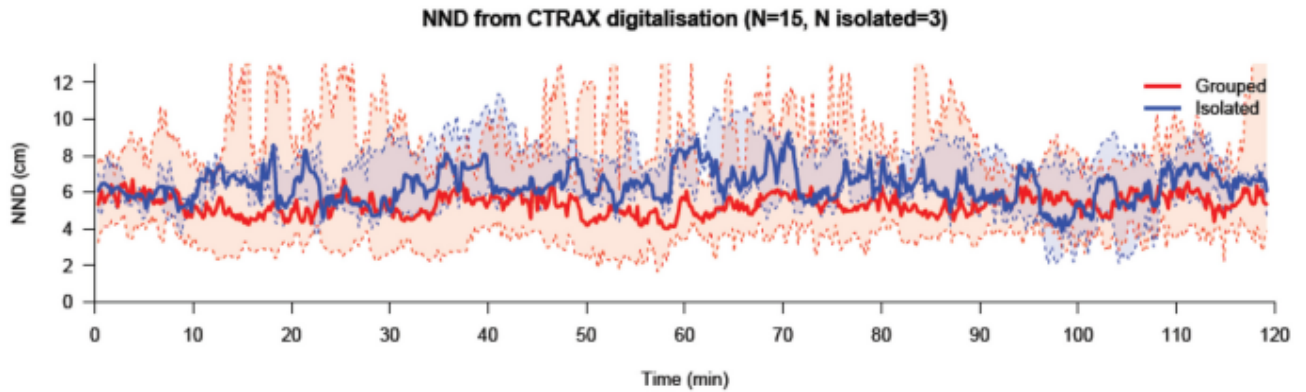


Fig. 2. Temporal variation of nearest neighbour distance (NND) in cm of isolated (grey) and crowded hoppers (black) in the arena analyzed with the Ctrax software. The plain lines indicate median values of 6 replicates, and dotted lines indicate the 95% corresponding distributions

Table 1. Comparative analysis of mean values of nearest neighbor distance (NND) for both treatments (isolated vs crowded reared) per time interval from Ctrax software digitalization. (sd: Standard deviation)

Time Interval	mean NND isolated	mean NND crowded	sd NND isolated	sd NND crowded	T-stat	P value
0–20	7.024	5.516	1.396	1.534	19.408	1.44E-074
20–40	6.797	5.283	1.390	1.396	20.631	4.79E-083
40–60	6.598	4.720	1.420	1.279	26.367	4.46E-125
60–80	6.879	5.168	1.536	0.920	25.648	1.36E-115
80–100	6.688	5.430	1.598	1.207	16.854	6.04E-058
100–120	6.171	5.398	1.505	1.119	10.243	1.52E-023

Likewise, with hand digitalization, the main values of NND (Fig. 3) were smaller for mass reared (from 4.789 to 5.628 cm) than isolation-reared (from 6.258 to 7.193 cm) hoppers and throughout the time of the experiments (Table 2). However, these NND from hand digitalization did not differ significantly from the NND measured with Ctrax software digitalization (Table 2).

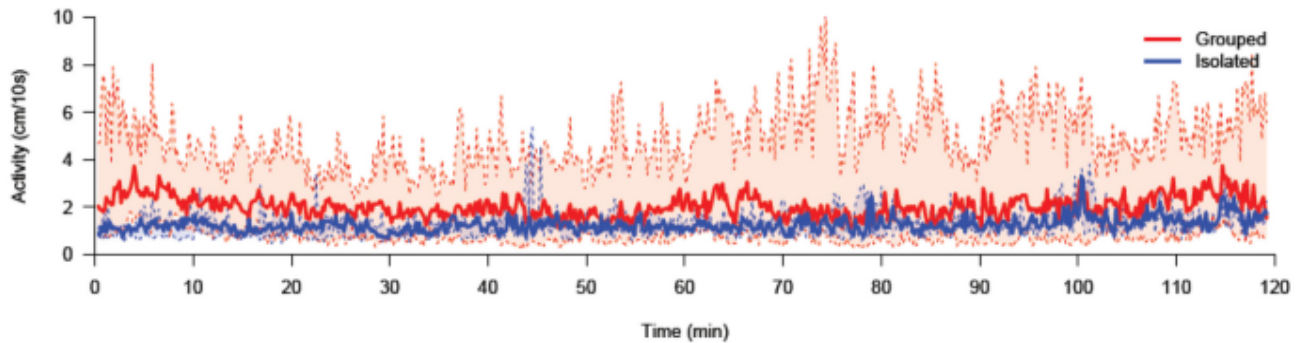


Fig. 3. Temporal variation of nearest neighbour distance (NND) in cm of isolated (grey) and crowded hopper (black) in the arena analyzed with hand digitalization. The plain lines indicate median values of 6 replicates, and dotted lines indicate the 95% corresponding distributions

Table 2. Comparative analysis of mean values of nearest neighbour distance using hand digitization (NNDh) for both treatments (isolated vs crowded reared) per interval of time and in comparison, with corresponding Ctrax software digitalizations (COMP)

Time Interval	mean NNDh isolated	mean NNDh crowded	sd NNDh isolated	sd NNDh crowded	T-stat	P value	COMP isolated T-stat	COMP isolated P value	COMP crowded T-stat	COMP crowded P value
0–20	6.780	5.628	0.987	1.543	3.082	0.004	1.172	0.252	-0.347	0.732
20–40	7.193	5.624	1.336	0.930	4.723	0.000	-1.424	0.167	-1.733	0.095
40–60	7.021	4.789	1.248	0.839	7.271	0.000	-1.625	0.117	-0.386	0.702
60–80	6.778	5.145	0.979	0.846	6.182	0.000	0.485	0.632	0.133	0.896
80–100	6.546	5.581	1.088	1.275	2.821	0.007	0.615	0.544	-0.572	0.573
100–120	6.258	5.447	1.096	1.159	2.489	0.016	-0.375	0.711	-0.206	0.839

Movements of individuals as an activity measure

The analysis of the mean distance covered by individuals within 10 s as a proxy of activity showed a difference in behaviour between both treatments. The mass reared hoppers were more active than the isolated-reared hoppers (Fig. 4). This difference was sharp at the beginning of the experiment, at least during the first 40 min. Through the following 80 min, the median values of activity of isolated-reared hoppers increased but did not reach the values of mass reared hoppers. The 95% upper limit of the activity distribution of isolated-reared hoppers was also higher during the last 80 min but still very rarely over the corresponding 95% upper limit of the mass reared hoppers. The statistical analyses confirmed that the differences in activity between isolated and mass reared hoppers stayed significant throughout the 120 min (Table 3).

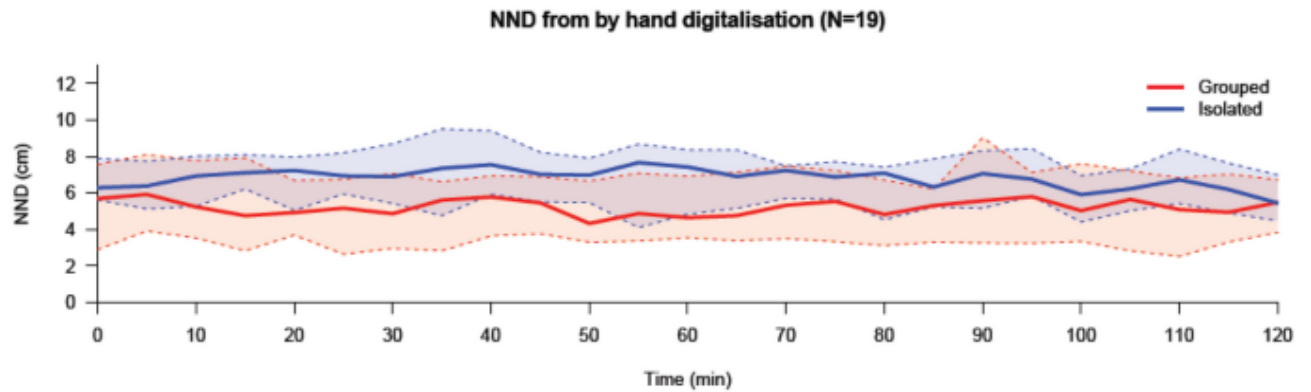


Fig. 4. Temporal variation of the distance moved by individuals over 10 s (cm/10 s) as a proxy of activity of isolated (grey) and crowded (black) hoppers in the arena. The plain lines indicate median values of 6 replicates, and dotted lines indicate the 95% corresponding distributions

Table 3. Comparative analysis of mean values of the proxy of activity (ACT) for both treatments (isolated vs. crowded reared) per time interval from Ctrax software digitalization

Time Interval	mean ACT isolated	mean ACT crowded	sd ACT isolated	sd ACT crowded	T-stat	P value
0–20	0.985	2.637	0.499	1.293	-31.856	0.000
20–40	1.003	2.205	0.573	1.030	-27.355	0.000
40–60	1.365	2.216	0.945	1.137	-15.447	0.000
60–80	1.308	1.996	0.834	1.187	-12.726	0.000
80–100	1.433	2.354	1.031	1.342	-14.611	0.000
100–120	1.596	2.832	0.902	1.449	-18.569	0.000

Discussion

Detecting distinguishable attraction or avoidance between individuals from seemingly random and conflicting behaviours requires a suitable method in a restricted area. Reproducing this method could be the best way to validate a scientific hypothesis. To this end, we did this experiment, which was conducted with a slight improvement of the previous study of Cisse et al. (2015) and a different locust species. The results showed that it is possible to distinguish the locust behavioural responses of the two phases from the analysis of the individuals' spatial positions in a circular arena. The video tracking confirmed that isolated-reared locusts are less active than mass reared ones. Also, isolated-reared locusts showed avoidance of each other with more considerable inter-individual distances, while mass reared locusts displayed attraction to conspecifics with shorter inter-individual distances.

These results were consistent with the previous study on *Schistocerca gregaria* (Cisse et al. 2015) and confirmed the behavioural disparity depending on the phase, which has been argued in several studies (Ellis 1953; Pener and Simpson 2009; Tanaka and Nishide 2013; Cullen et al. 2017). They first allowed a striking observation of the activity level, one of the characteristic traits for differentiation between solitary and gregarious locusts, as a preponderant indicator in the analysis of the aggregation and synchronization of mass movements in *Locusta migratoria* (Uvarov 1928; Lecoq 1975, 1978). In the field, the increase

in locust numbers is a stimulator of increased activity due to contact between each other (Ellis 1953). The aggregation behaviour is learned gradually and depends on the habituation of the hoppers by mutual touching (Peggy and Ellis 1962; Simpson et al. 2001).

Our approach was also complementary to the behavioural quantification method, as described by Roessingh et al. (1993) in *Schistocerca gregaria*. Nevertheless, we did not analyze the other ethological parameters (e.g., walking time, grooming frequency) to describe the phase behaviour related to the activity or the attraction/repulsion behaviour facing a stimulus group. However, we proposed a simple method that allowed behavioural analysis of large numbers of locusts in a restricted area, improving the method of Ellis (1953) with spatial statistics.

Moreover, our results did not make it possible to verify if the change of the activity precedes the change of aggregation/repulsion to other locusts. This latter hypothesis was observed in a previous study (Cisse et al. 2015). This dissimilarity could be related to biological material, suggesting different responses from *Schistocera gregaria* and *Locusta migratoria*. Indeed, we know that desert locust is very sensitive to changes in density with a lower density threshold of gregarization (Popov et al. 1991; Desanges 2006). Contrariwise, the *Locusta migratoria* has lower density sensitivity with a higher density threshold of gregarization (Desanges 2006). Despite these differences between the two species, we could see the differences in the nearest neighbour distance (NND) between phases with the same methodology applied to both species. Here, the median NND of mass reared hoppers was 5.161 cm, while the median NND of isolated-reared hoppers was 6.677 cm. The same trend was previously observed with *S. gregaria*, where the median NND of mass reared hoppers was 5.57 cm while the median NND of isolated-reared hoppers was 6.58 (Cisse et al. 2015). Accordingly, both species showed similar behaviour in a circular arena. As argued by Peggy and Ellis (1962), the grouping behaviour in larvae of Migratory Locust could change in relation to age, rearing conditions, color at hatchlings and parents rearing conditions and varies depending on locust species. Our study involved mass reared hoppers and isolated-reared hoppers of the 3rd development stage, and all derived from a crowded breeding line. The average duration of isolation was 7 days after hatching. Even with short isolation time, distinct behaviours were observed with mass reared hoppers. This feature is consistent with previous work that argued that a few hours are enough to observe some phase change traits in locusts (Tanaka and Nishide 2013; Rogers et al. 2014). Long-term isolation, especially at the parental level, could reveal a more noticeable behavioural difference (Ellis 1959; Peggy and Ellis 1962; Roessingh et al. 1993; Maeno and Tanaka 2009; Chapuis et al. 2010). The hatchlings we used as “solitarious” were from a gregarious line, suggesting potential epigenetic effects of the mothers (Hunter-Jones 1958; Bouaïchi and Simpson 2003; Cullen et al. 2017). Despite this, we observed a different behaviour with those coming directly from a group breeding.

Also, *Locusta migratoria* has remarkable ecological plasticity, which explains its wide geographical distribution (Launois-Luong and Lecoq 1996). Structural differences have been reported between the different geographical subspecies (Uvarov 1966; Farrow and Colless 1980; Pardo et al. 1993; Chapuis et al. 2009, 2011). However, extreme phase differences are encountered in the field, whatever the subspecies of *Locusta migratoria* (Pener and Simpson 2009) and transitional states between the two extremes are numerous (Albrech 1967; Rogers et al. 2014). This suggests that, although our methodology seems effective for characterizing

phase behaviour in locusts, it is better to continue to test with other larvae development stages for more validation.

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Conflict of interest

We have no conflict of interest to disclose.

Data Availability

The data that support this study will be shared upon reasonable request to the corresponding author.

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