

Research Article

Phase-Dependent Color Polyphenism in Field Populations of Red Locust Nymphs (*Nomadacris septemfasciata* Serv.) in Madagascar

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Received 26 May 2010; Accepted 12 August 2010

Academic Editor: Maria Marta Cigliano

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Pigmentation of the Red locust hopper, *Nomadacris septemfasciata* Serv., was studied in natural conditions in Madagascar in relation to population density. More than one thousand hoppers were collected and described according to a semiquantitative method. A typology is proposed, strictly reflecting the increase in population densities. This correctly translated the progressive evolution of a solitary state into a gregarious state, while passing through several intermediate transiens stages. According to their density, hopper populations consist of a mixture, in various proportions, of several pigment types. The gregarization threshold is estimated at 100,000 hoppers/ha. A slight black spot on the hind femur is the first sign of gregarization. These results should improve the reliability of the information collected by the Malagasy National locust centre when surveying this major pest. They question the rapidity of the gregarization process in natural conditions as well as the stimuli involved.

1. Introduction

Locusts are acridid species that exhibit density-dependant phase polyphenism and/or an ability to form marching hopper bands and/or flying swarms resulting in outbreaks and plagues. Individuals are either of two extreme phenotypes: solitary or gregarious [1, 2]. This polyphenism is continuous and all the intermediate stages, transiens, congregans or dissocians, are found between the two extreme phases, depending on the direction of the transformation. Induction of phase transformation can occur at any stage of development of the locust including the larva and the imago. It can be strengthened through generations and is reflected by a suite of changes in behaviour, morphometry, color, development, fecundity, and endocrine physiology (see recent reviews in [3–7]). Better understanding of locust phase polyphenism has an obvious applied potential and could lead, in the future, to nonconventional locust control measures as a substitute for the chemical insecticides in use [5], but increasingly challenged because of their environmental impact [8, 9]. Currently, the precise characterization of the phases, and especially the intermediate transiens, is crucial for the effective implementation of preventive strategies

against these locust pests, which require intervention as early as possible [10–13]. The transiens phase marks the first stages of the gregarization process. In the progressive development from remission periods to invasive periods, an understanding of the transiens phase can allow early detection and measurement of the degree of severity of the locust situation.

In nature, behavioural changes are often the first characteristic observed as a result of a gathering of individuals caused by external causes such as wind convergence, surface restrictions related to phenomena such as floods, and resource distribution [14–18]. This characteristic is difficult to precisely quantify for the intermediate transiens stages. Morphometry remains the best method to estimate the degree of phase transformation of an individual or a population. Morphometric charts can be used to monitor the gregarization process over generations [2, 3, 19]. In hoppers, only the color characteristics can be used. The coloring is one of the most obvious signs of the phase transformation in locusts [5]. Several studies have been carried out on the nature of the pigments involved, the underlying physiological mechanisms, and the influence of environmental conditions [2, 3, 20–23]. The color characteristics of the solitary and gregarious phases have been shown numerous times (see,

e.g., Stower [24] for the Desert locust *Schistocerca gregaria* Forskål; Faure [25, 26] for the Red locust *Nomadacris septemfasciata* Serville 1838; Albrecht [20], Lecoq [27], Popov [28] for the Migratory locust *Locusta migratoria* L. 1758). The transiens phase remains, however, much less well documented, especially for the hoppers. Often, in the literature, the near infinite number of intermediate colors between the solitary and the gregarious phases of these individuals is just mentioned. In the recent review by Pener and Simpson [5] the word transiens (or transient) appears 10 times only, when gregarious and solitary are mentioned respectively, 560 and 440 times. Moreover, the phase transformation threshold is widely ignored. In nature, this threshold corresponds to the population density at which the interactions between individuals are large enough to allow the phase transformation process to start. It is sometimes given on the basis of an expert opinion without any results of specific observations [29]. The very validity of this concept is sometimes questioned because it also depends on the insect development stage and on the vegetation density [30]. This is crucial information from both an operational perspective to better manage locust preventive control and from a theoretical point of view to allow further detailed field studies on the phase transformation process determinism.

The various difficulties in the characterization of transiens are particularly noted for the Red locust. In this species, despite various studies that have contributed to describing the pigmentation of the solitary and of the gregarious stages [25, 26, 28, 31–33], the transiens remains poorly characterized and the phase transformation thresholds have never been established. More generally, phase polyphenism in the Red Locust is poorly understood and has rarely been proven experimentally and—in comparison to Desert and Migratory locusts—just a few papers are available for this species (see for instance [34–36]). The main effects of increased density on *Nomadacris* as revealed by laboratory work, were summarized by Uvarov a long time ago [2], and further research is obviously required [5]. In practice, the information collected by the locust services on the transiens phase is often unreliable [37]. We propose to clarify the color characteristics of the hopper individuals of this species in relation to population density. This study aims to provide a better understanding of the phase transformation thresholds and to improve the implementation of monitoring and preventive control of this species. This work was carried out in the field in Madagascar where this locust is a major crop pest.

2. Materials and Methods

2.1. The Red Locust. The Red locust is well known throughout central and southern Africa [38, 39]. Some isolated populations can also be found in the lake Chad basin, the central delta of the Niger river in Mali, and the Cape Verde Islands [40]. The species undergoes phase transformation and its outbreak areas are mainly located in the Great Lakes region of East Africa, in Tanzania, Zambia, Malawi and Mozambique [41, 42]. Since the last great invasion of 1929–1944, which affected most African countries south of

the equator, the species is controlled by an international organization, IRLCO (International Red Locust Control Organization) [43]. Infestations are now less frequent and are mainly focused in the reproduction areas, far from the cultivated areas [44]. Large outbreaks occurred, however, between 1994 and 1996 [42, 43, 45, 46] and more recently in 2009 [47, 48].

In Madagascar, the Red locust is also a major pest and outbreaks are frequently observed with formation of hopper bands and swarms. No widespread invasion of the island has ever occurred as was frequently the case with the Migratory locust [49] whose last plague ravaged the Island between 1997 and 1999 [11]. The problem is now managed by the National Anti-Locust Centre as part of a crop protection strategy [40, 50, 51]. In Madagascar, the lifecycle of the Red locust has only been documented for the Betsioky-Sud region, where this species produces just one generation per year [52–58], as in the rest of Africa. Mating and egg laying take place in November and December, at the onset of the rainy season, which lasts until April. Females generally lay eggs twice or three times, with a clutch of 20–100 eggs for gregarious locusts and 20–195 eggs for solitary locusts. The eggs hatch after 24–36 days of incubation. The hoppers begin to appear in December. The hopper development passes by 6 instars for the gregarious individuals (1 to 6) and 7 instars for the solitary (numbered 1, 2, 3, 4, 4a, 5, and 6 in order for the last instar to always carry the same number, the extra instar being before the reversal of the wing rudiments, between instar 4 and 5) [34]. The hopper development period lasts almost 2 months, ranging 50–70 days and the new generation of adults appears in April. They enter diapause to survive through the dry season (April–September), in refuge zones located away from breeding areas. Important seasonal migrations of solitary populations take place between dry season refuge zones (where population densities are low) and rainy season breeding zones (where the populations concentrate and reproduce and where outbreaks are frequently observed) [59]. Samples of hoppers were collected from this latter area, where the first manifestations of gregariousness may occur (behavioral changes in the parental adults, and behavioral, pigmentary, morphological changes etc. in the offspring).

2.2. Sampling and Description of Hoppers. Red locust hoppers were collected in south-western Madagascar in a vast area well-known as the breeding area of this species. The samples were taken during two successive rainy seasons from January to March in 2007 and in 2008. During the two sampling periods, we continuously (each hour) recorded the air temperature and the relative humidity in one location in the sampling area (near Betsioky-Sud). Both parameters were not very variable, during one sampling period as well as from one year to another (temperatures 2007/2008: min 22, 7°C ± 1, 4/23, 1°C ± 1, 5; max 35, 1°C ± 3, 1/37, 0°C ± 4, 2; average 27, 8°C ± 1, 7/28, 9°C ± 2, 3; air humidity 2007/2008: min 39, 8% ± 14, 4/34, 4% ± 17, 7; max 82, 5% ± 7, 9/80, 2% ± 8, 4; average 64, 1% ± 10, 9/59, 1% ± 13, 3).

The sampling sites were chosen based on the information provided by the National Anti-Locust Centre on the presence

of locust hoppers and their density. At each site, thirty hoppers were collected. The hopper density was evaluated by counting one hundred sample surfaces of one square meter each using a classical method commonly used by scouts from the locust centre [60, 61]. These hopper populations were derived from migrant adults arriving in the breeding area at the start of the rainy season and whose phase status was described broadly as solitary as shown by survey data from the National Anti-Locust Centre (3741 observations conducted on the whole of south-western Madagascar in 2006 and 2007 on the parental populations). Some populations in densities above the gregarious threshold, however, were observed (13 in all, including 4 light swarms at a density of between 160,000 and 200,000 imagos per hectare).

For each hopper, the stage was determined by overall size, the size and the orientation of the wing pads, the number of eye stripes, and the color characteristics recorded using a standardized method. Only phase color (density) polyphenism and green/brown (humidity) polyphenism exist in the Red locust [5]. The latter is relatively limited as the hoppers of the single annual generation were still developing in relatively close conditions at the heart of the rainy season in lush vegetation. The proportion of green hoppers diminished late in the rainy season [57]. In cages, homochromy has sometimes been observed in solitary hoppers [26]. Regarding the phase color polyphenism, the descriptions in the literature concern essentially solitary and gregarious individuals [25, 26, 28, 31–33]. For the transiens phase, information is scarce and mainly concerns the transiens dissocians [31, 33].

The characters finally selected were the background color (GC) and the degree of melanisation of the cephalic capsule (H), the degree of melanisation of the compound eyes (E) (with more or less visible stripes), background color of the pronotum (GP) and the degree of melanisation of its dorsal carina (CP) and lateral sides (LP), the degree of melanisation of the wing pads (W), and the presence and extent of a black spot on the distal part of the upper outer carina of the posterior femur (F). The latter criterion was supposed to be one of the first signs of gregariousness when the population density increases. The black abdominal maculation, difficult to quantify, was not considered. These eight criteria were recorded in the field using a semi-quantitative method (Figure 1). For E, H, CP, W, LP, and F, the extent of black pigmentation was coded 0 for absence of black pigmentation, 2 for a well-marked black spot and 1 for an intermediate situation. General pigmentation was recorded as green, brown, or orange for the cephalic capsule (GC), and as green, brown, or yellow for the pronotum (GP). Each hopper was individually identified and photographed under standard conditions for later checking of the rating criteria.

2.3. Data Analysis. The results were analyzed using the Addinsoft XLSTAT data analysis software (1995–2010). The data table [hoppers \times color variables] containing the value of the different variables (semi quantitative) for each of the hoppers observed was converted into a disjunctive table (each nominal variable comprises several levels and each of these levels is coded as a binary variable). The latter was

subjected to a Multiple Correspondence Analysis (MCA) to highlight the relationships between the various color variables, on the one hand, and between the hoppers on the other hand, according to their similarity [62]. The hoppers and the variables were then classified according to their coordinates on the first factorial axes of the MCA using a hierarchical clustering method (Euclidean distance, Ward's aggregation method). A typology of the hoppers, from the most solitary to the most gregarious, was constructed on the basis of the results of this classification. Finally, each class of hoppers was related to the population density value in which they were most frequently observed. This helped establish the phase transformation threshold, that is to say, the population levels from which one hopper class moves to another, solitary forms to more and more gregarious forms (or more exactly, from population consisting of a mixture of different color types in varying proportions to another).

3. Results

3.1. Hoppers Pigmentation. A total of 1139 hoppers were collected and their color characteristics were described, respectively, 36, 129, 123, 283, 233, and 343 hoppers of 1, 2, 3, 4 (including 4a), 5, and 6 instars. These hoppers were collected in 42 localities where hopper densities were (on a very regular density gradient) less than one hopper (solitary populations) to several hundred hoppers per square meter (gregarious hopper band) (Figure 2). For densities greater than 150 hoppers/m², no accurate count was possible and this class included densities ranging from 150 to several hundred hoppers per square meter.

The hoppers collected from low-density populations (less than one hopper per square meter) were characteristic of the solitary phase with a general green background coloring on all parts of the body (sometimes slightly yellowish) and a lack of black pigmentation (Figure 3). The pigmentation was generally very similar in all individuals with low variability. Rare individuals with a general brown background color were sometimes observed and were regarded as solitary individuals within the traditional framework of the green/brown polyphenism (as is the case with the Migratory locust, e.g.). However, even if some of these individuals were found in low-density populations (<1/m²), they were occasionally collected in relatively high-density populations of about 20–69 hoppers per square meter. Their status remains uncertain, but these hoppers (10 in all) represented only 0.9% of the individuals collected.

As the population density increased, changes in pigmentation and pigment diversity increased. More numerous yellowish or orange areas appeared as well as melanised areas. In high-density populations (100/m² and more), the pigmentation was typical of the gregarious phase, which has been described by various authors: the compound eyes were completely dark and the eye stripes were invisible, the cephalic capsule is almost completely melanised, the general background color of the hopper was bright orange and a large part of the body was marked with highly developed black spots (Figure 3). Between these two very contrasting solitary and gregarious states, color changes

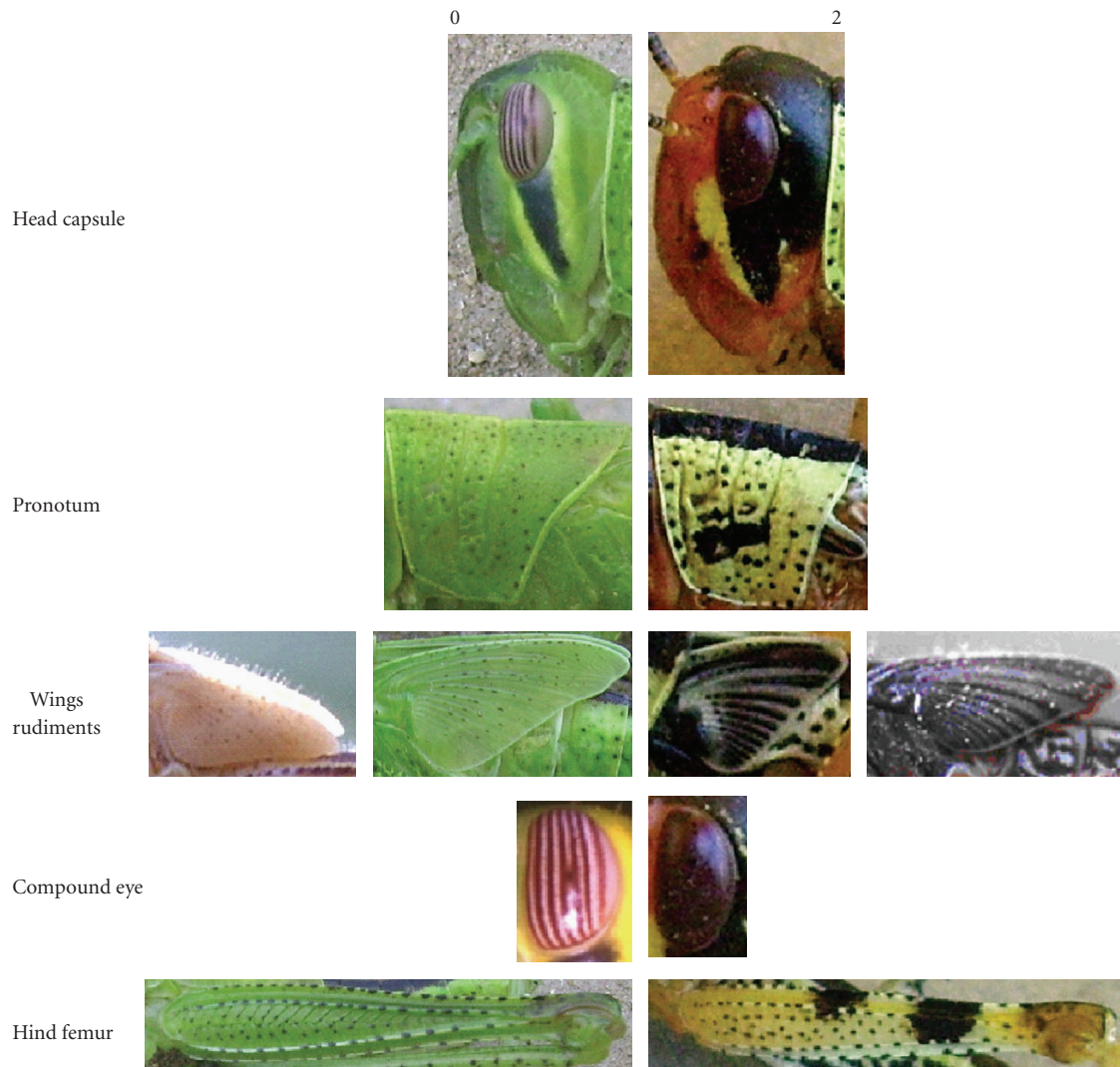


FIGURE 1: Color patterns and morphological variables selected to characterize the pigmentation of Red Locust hoppers. Note that the subocular stripe is a constant characteristic of the Red Locust but, in case of gregarisation, it tends to disappear under the general black pigmentation of the posterior part of the head. Photos: M. Lecoq, A. Chamouine and M.H. Luong-Skovmand.

became more pronounced and appeared gradually in relation to density, corresponding to individuals that could generally be described as transiens (Figure 3). These changes primarily concerned the femoral spot (F), the dorsal carina of the pronotum (CP), the compound eyes (E), and to a lesser extent, the cephalic capsule (H). With densities higher than $100/\text{m}^2$ the melanisation was well marked for all the variables (E, CP, LP, W, F equal to 2 in almost 100% of cases). A progressive change in the background color of the pronotum (GP)—from green to yellow from low to high densities—was also recorded, as well as a change from green to orange for the background color of the cephalic capsule (GC).

3.2. Hoppers Typology. MCA demonstrated that the data were highly structured with the first two factorial axes totaling almost 90% of the total inertia of the cloud of points (Figure 4). The plane determined by these first two

axes served to underline the correlation between hopper pigmentation and hopper population density (density was introduced in the analysis as an additional variable, that was not included in the calculation of the inertia of the cloud of points, but projected on the axes). The first axis alone groups 82.4% of the inertia. On this axis, there is an opposition between the absence of melanisation and the green colors, on the one hand, and a strong melanisation and yellow and orange colors, on the other hand. This differentiated the solitary individuals very schematically from those with gregarious characteristics. Along this axis, the hopper density classes ranged regularly from low densities on the negative side of the axis to high densities on the positive side. Axis 2 groups 5.9% of the inertia and shows an opposition between extreme color characteristics (0 and 2 for melanisation, green and orange for background color) and the intermediate values

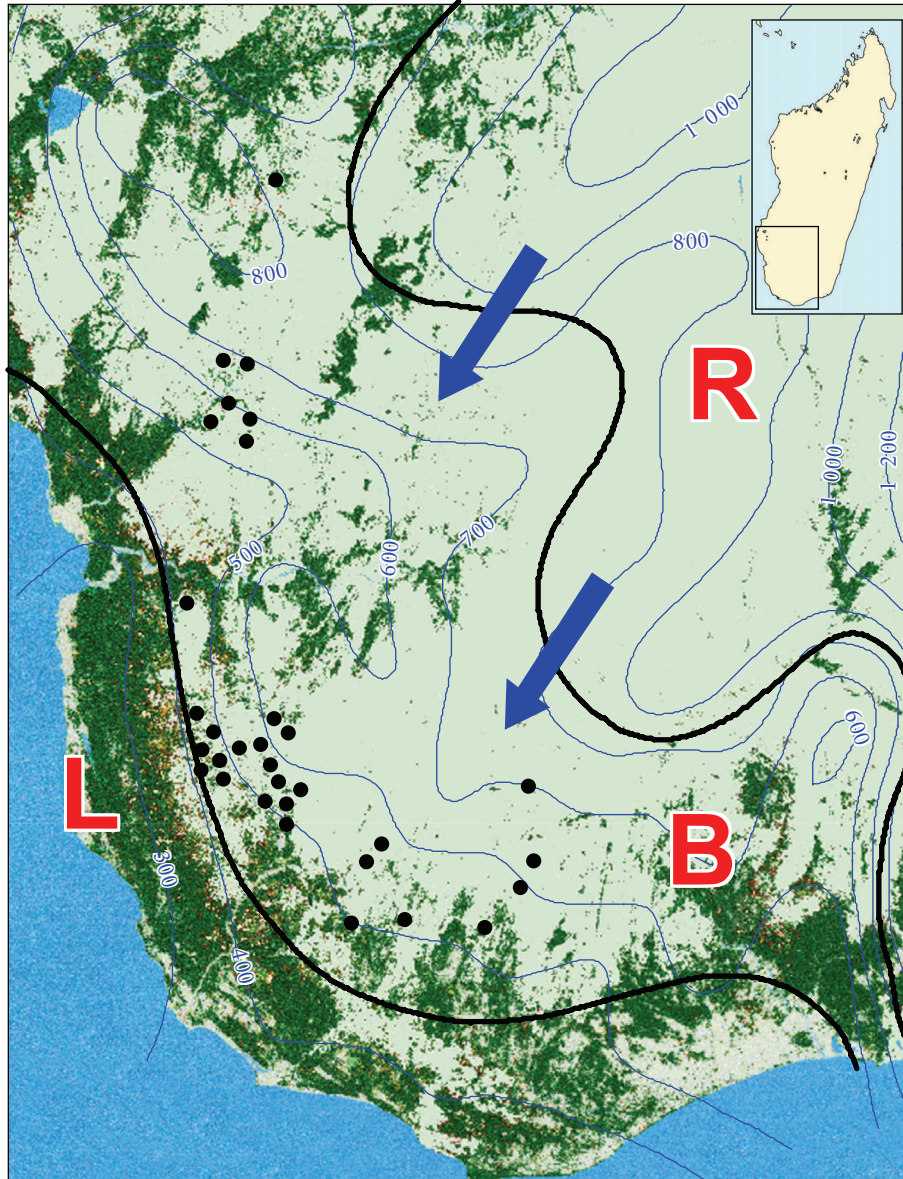


FIGURE 2: Location of the locust hoppers sampling sites in 2007 and 2008 in southern Madagascar. R: dry season refuge zone; B: breeding zone; L: unsuitable southernmost border zone. Green areas: dry forest. Blue lines: isohyets (mm). The arrows underline the orientation of the migrations of maturing adult populations at the beginning of rain season (according to Lecoq et al. [59]).

(1 for melanisation, green-orange, yellow and yellow-orange for the background color). This axis thus underlines the first demonstration of color polyphenism. Finally, axis 3 with only 2.9% of the inertia is entirely determined by individuals with a brown background. These results were valid regardless of the hopper instar. The same analysis (MCA) conducted either on older hoppers (4, 5 and 6) or on young hoppers (1, 2 and 3) led to exactly the same results as well as for tests conducted separately on data from 2007 and 2008 (results not shown).

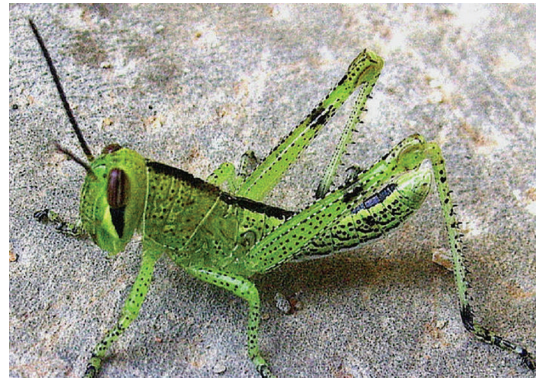
Classification of individuals according to their coordinates on the first five factorial axes provided a hopper typology to distinguish 15 types. This could be correlated with population density where the hoppers were

collected. The color characteristics changed very gradually with increasing density. A regular gradient of color types existed from types 15, 8, and 13, showing the characteristics of low-density populations representing the solitary types (especially the most abundant type 13), to types 6 and 9 that were found in populations where the density was higher than 60 hoppers/m², and more generally, those where the density exceeded 150 hoppers/m², and represented typically gregarious individuals. Between these two extremes, the other 9 types corresponded to intermediate situations concerning both color and density, and transiens-type hoppers (Figure 5). Each hopper class was not therefore associated with a specific population density, but its frequency increased and then decreased steadily with density. Thus, class 5 was



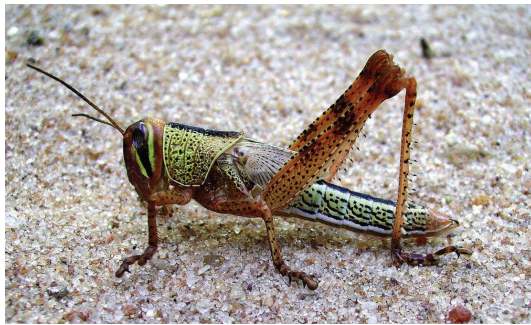
Solitarious

(a)



Solitaro-transiens

(b)



Transiens

(c)



Gregarious

(d)



(e)

FIGURE 3: Examples of Red Locust hopper polyphenism (above) and gregarious hopper band (below) observed in February 2008 in the southern part of Madagascar (Mahafaly plateau). Photos: M.H. Luong-Skovmand (solitarious and gregarious) and A. Chamouine (solitaro-transiens, transiens and hopper band).

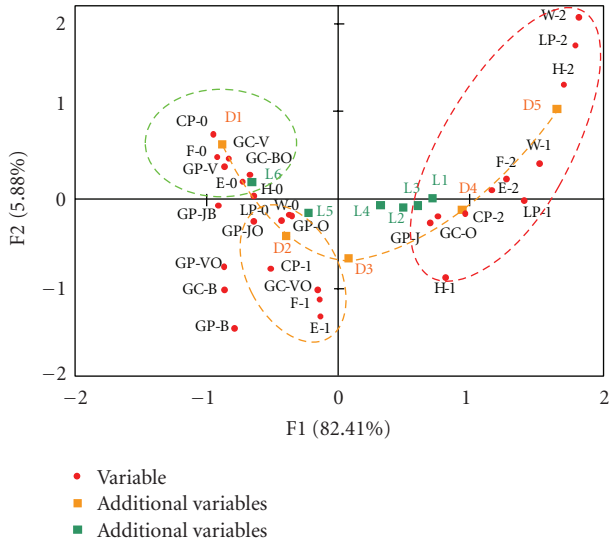


FIGURE 4: Result, in terms of the first two factorial axes, of the multiple correspondence analysis carried out on the table [individuals × variable pigment]. Ellipses surround variables characteristic of the solitary, solitarno-transiens/transiens, and gregarious populations. The brown individuals, from dubious status, isolate themselves on axis 3. Codification of the variables (red dots): (1) variables related to the black pigmentation (0, 1 or 2 according to the melanisation intensity): compound eye (E), cephalic capsule (H), median carina of pronotum (CP), wings rudiments (W); lateral black spot of pronotum (LP), black spot on hind femur (F); (2) variables related to the general color of the tegument (V, green; B, brown; O, orange; J, yellow): cephalic capsule (GC) and pronotum (GP). Variables introduced into the MCA as additional elements: D1 to D5, density of the hopper population (D1 < 10, D2 = [10–30], D3 = [30–70], D4 = [70–100], D5 > 100/m²) (orange squares); L1 to L6, hopper instars (green squares).

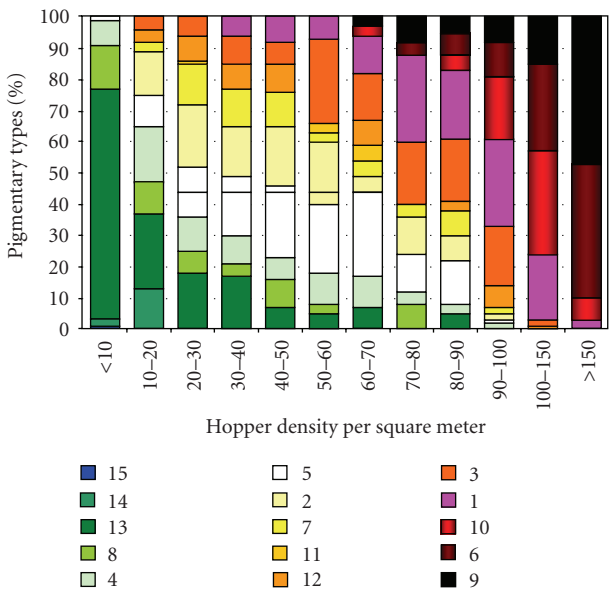


FIGURE 5: Relationship between the 15 color types and hopper densities. In X-coordinate: density classes; in ordinate: percentages of the various color types (1 to 15).

present at low levels for densities less than 10 hoppers/m², and it was more abundant in densities ranging from 20 to 30 hoppers, then steadily decreased in frequency. This type of hopper was not found at densities greater than 100 hoppers/m².

3.3. A Simplified Typology for Operational Purposes. In order to achieve a practical classification that is easy to use as part of locust population survey operations, the 15 color types were grouped into 4 types based on the classification results and according to their percentage of presence in the different density classes. The color types 15, 14, 13, 8, and 11, only present in low-density populations (<10/m²), were grouped into a single type which gathered together, in their diversity, populations that were typically solitary. Types 6 and 9 were virtually the only ones present in very high-density populations (>150/m²) and could be regarded as representative of the gregarious populations. Types 4, 2, 5, and 7, which were very similar and predominated the medium-density populations, corresponded to solitarno-transiens populations. Finally, types 12, 3, 1, and 10, also similar, predominated the population at densities slightly greater (70–100/m²) than for the previous types. These types could be grouped under the name transiens. These different types of hoppers can be distinguished easily and unambiguously on the basis of certain criteria for easy use in the field by the locust center scouts (Table 1). Thus, the appearance of the femoral spot signified the transition between solitary and solitarno-transiens populations. Wing-pad melanisation distinguished solitarno-transiens and transiens hoppers. Finally, maximal melanisation of all body parts signified the onset of the gregarious type. Ultimately, the criteria used could easily assign each hopper to a particular phase category, either solitary, solitarno-transiens, transiens, or gregarious.

The hopper populations consisted of a mixture of hoppers that may belong to different color types. The percentages of each category developed progressively: a high proportion of solitary individuals were found in lower density populations and higher densities had increasing proportions of solitarno-transiens, transiens and then gregarious individuals. Solitary, solitarno-transiens, transiens or gregarious populations could thus be classified on the basis of the dominant color types within the population.

3.4. Pigmentation and Population Density. Some color variables changed earlier than others to an increase in the hopper population density and could therefore be regarded as indicators of early signs of gregarization (Table 1). The eye stripes were still visible in half of the hoppers collected at a density of 30–70/m². The eyes were dark for most of the hoppers at a density of 70–100/m². Melanisation of the cephalic capsule, which started at 10–30/m², was especially marked at a density of 70–100/m². The background color of the cephalic capsule was green for most of the larvae at very low densities. The red-orange color became predominant only at a density of 30–70/m². Melanisation of the dorsal carina of the pronotum appeared at a density of 10–30/m² and half of the hoppers were strongly marked at a density

TABLE 1: Color characteristics of the four hopper types.

Characters	Hopper types			
	Solitarious $d < 10/m^2$	Solitiro-transiens $d = 10-70/m^2$	Transiens $d = 70-100/m^2$	Gregarious $d > 100/m^2$
E	0	0-1-2	1-2	2
H	0	0-1	0-1	2
GC	green or brown	green, green-orange, yellow or orange	orange	orange
CP	0-1	1-2	2	2
LP	0	0	0-1-2	2
GP	green or yellow	green or yellow	yellow	yellow
W	0	0	1	2
F	0	1	2	2

E: compound eye; H: cephalic capsule; GC: general pigmentation of the cephalic capsule; CP: median carina of pronotum; LP: lateral black spot of pronotum; GP: general pigmentation of the pronotum; W: wings rudiments; F: black spot on hind femur.

of $30-70/m^2$. Conversely, the lateral pronotal spot was very pronounced in only one third of the hoppers at a density of $70-100/m^2$. It was strongly marked in all the hoppers for densities greater than $100/m^2$. The background color of the pronotum, mostly green in individuals in very low densities, turned yellow in the majority of hoppers at a density of $10-30/m^2$. The darkening of the wing pad veins appeared later. It was significant in one third of individuals at a density of $70-100/m^2$. Above a density of $100/m^2$, all hoppers had strongly melanised wing pads. The femoral spot appeared at a density of $10-30/m^2$ and it was predominant in half of the hoppers at a density of $30-70/m^2$. It was present and strongly marked in all hoppers at high densities ($>100/m^2$). Finally, the first transiens hoppers appeared at a density of only $10-20$ hoppers/ m^2 (Figure 5).

4. Discussion

4.1. Characterization of the Hopper Phase. The results from our field study on Red Locust hopper pigmentation established a clear typology, which strictly reflected the increasing densities of the populations. This correlates with the results obtained by Gunn and Hunter-Jones [63] on the regular gradient of pigmentation in relation to hopper density in the Migratory locust under laboratory conditions. In our case, this gradient reflected the gradual development of individuals from the solitarious state to the gregarious state through several intermediate transiens stages. Up to nine transiens categories were distinguished. Finally, only two were selected for a practical classification to highlight the first key stage of the gregarization process represented by the solitiro-transiens individuals. For each density, hopper populations were composed of a mixture of several color types in varying proportions. The proposed criteria were simple and unambiguous. The information collected by the National Anti-Locust Centre in Madagascar on the phase status of hopper populations could thus become precise, reinforcing the reliability of the survey protocol on this species.

There was a possibility that environmental factors, other than population density, affected hopper coloration. For

instance, temperature affects dark color patches in many acridids, especially in locusts [21]. In our case, temperature and humidity were not very variable during the sampling periods. The same results were obtained in 2007 and 2008 whatever the ecological conditions showing that population density was more important than any other factor—in our field conditions in Madagascar—to determine the coloration of hoppers of the Red Locust, contrary to an early statement by Lea and Webb in 1939 [64].

Our results confirmed (although only the pigmentation aspect was considered, which is just one component of phase polyphenism), that all hopper phases are present in Madagascar: the solitarious, all transiens-intermediate stages, and true gregarious hoppers were, in all respects, similar to those previously described in the literature, both in pigmentation and behavior (well-established and large, dense hopper bands of several hundred hoppers per square meter). These results therefore contradict the hypothesis by Roblot [65] and Roy [66], in force for almost half a century, according to which, as the environment is assumed to be less favorable to the Red locust in Madagascar as compared to Africa, only solitarious and transiens forms were able to exist on the island. This concept was so ingrained in the mentality, that the National Anti-Locust Centre in Madagascar deleted the term “gregarious” from the observation forms; only solitarious or transiens individuals were recorded. This is obviously the best way to avoid observing gregarious individuals. Our results complemented recent studies (based on morphometric measurements) showing that the gregarious phase amongst the imagos was indeed present in Madagascar from the extreme south to the extreme north of the country [67]. A new gregarious area has moreover recently been identified following major outbreaks that occurred from 1999 to 2003 in the far north, surely as a result of intensive deforestation leading to the creation of new suitable biotopes [67, 68].

4.2. The Gregarization Threshold in Red Locust Hoppers. Our results showed that the typology of hopper populations is strictly a reflection of hopper density. The color changes marking a first phase change were noted in the hoppers found in populations where the density is 10 hoppers

per square meter. The first real gregarious hoppers are found, occasionally, from 60–70 hoppers/m² and become predominant from 150/m². Thus, the gregarization threshold can be estimated at about 100,000 hoppers per hectare. To our knowledge, this is the first indication of this type in the Red locust. For adults, this threshold has been recently estimated to be around 5,000 individuals per hectare by Franc et al. [67]. In comparison, the threshold is estimated at 2,000 adults/ha for the Migratory locust [69]. For the Desert locust, the threshold is estimated at 250–500 hoppers per hectare and varies between 5 and 0.5 hoppers/m² from the first to the fifth instar [29]. For the Red locust, the threshold is probably very likely to be modulated according to the hopper instar. The value quoted above was an average for all of our sampling (1th to 6th instars). Presumably it was lower in the 6th instar and higher in the first, which should be verified on a larger sample.

The gregarization threshold may be reflective of the hopper environment, particularly the structure of the vegetation. The latter may be more or less heterogeneous and may promote local concentrations of populations. In general, the distribution of resources such as food, favorable areas of microclimate, and roosting sites are all factors that may help promote gregariousness as has been shown especially in the Desert locust [16–18]. However, the Saharan habitats of the Desert locust, a plurivoltin species, can be very diverse, both in space and time. On the contrary, the hoppers of the only annual generation of the Red locust in Madagascar varies between January and March, within the breeding area in the south-west, in a lush, dense vegetation (100% coverage, plant height between 40 and 80 cm on average) whose structure is very similar from one year to the other. We believe that the threshold concept takes on certain significance and is of considerable value for the local antilocust survey service, even if the figures are only a rough estimate.

Finally, it is interesting to compare our threshold values to those recorded experimentally for the density at which the coordinated marching behaviour of the gregarious populations appears. Collett et al. [18] has shown experimentally, in the third hopper instar of the Desert locust, coordinated movements that are well marked at densities above 74 hoppers/m². However, at densities below 18 hoppers/m², no coordinated movement is noted. Even if the species and conditions were very different from ours (hoppers in the field in dense vegetation compared to hoppers in a circular arena without vegetation), it is interesting to note that our observations give similar values with a phase transformation threshold estimated at 10 hoppers/m² and the emergence of real gregarious hoppers from densities of 60–70 hoppers/m². This could be the result of an identical “radius of influence”, whatever the circumstances and regardless of the stimuli involved. Differences in the gregarization threshold for Migratory, Red and Desert locusts could therefore be the result of the respective structures of these three species’ habitats. For adults, the lowest gregarization thresholds were indeed noted for the Desert locust living in habitats where vegetation is scarce and often in clumps and highest for the Red locust living in environments with much wetter, tall, and dense vegetation.

4.3. Phase Transformation Rapidity and Parental Antecedents. The fact that from solitarious parental populations we can obtain hoppers with perfectly gregarious color characteristics in the next generation may question the rapidity of the gregarization process in the Red locust. Can we consider a parental effect on our results? We know that phase characteristics are transmitted to offspring, a phenomenon well known in the Desert locust and the Migratory locust [70–74]. In Madagascar, the early stages of phase transformation are often initiated at the beginning of the rainy season when solitarious populations migrate from the dry season refuge areas to the rainy season breeding areas. Such a phenomenon is observed in the Migratory locust [49, 60] as well as in the Red locust [59]. These migrations often lead to sudden and rapid increases in adult densities allowing the appearance of the first behavioral manifestations of gregarization. The density shock suffered by females during laying can be inherited and affect the phase of the descendant and, in particular, the expression of color polyphenism in the hoppers.

Such a parental effect could explain the rapidity of the process observed in the hoppers. Even if the parent populations appear to have been mostly solitarious, observations conducted by the National Anti-Locust Centre have shown the presence of some population densities above the gregarization threshold and a few swarms. In early 2006, in the dry season, the average density in south-western Madagascar was 94 adults/ha (max 680). In the early rainy season of 2006–2007, the average density increased to 664/ha (with one swarm at 160,000/ha), then decreased to 272/ha in the early dry season of 2007 (with four swarms and nine cases where the density exceeded the gregarization threshold of 5,000 adults per hectare). All transients or gregarious hoppers could descend from parent populations that have already experienced, to varying degrees, a density shock in their history when laying or early in their development over a number of generations. This is impossible to determine, but it would explain the wide range of phase conditions registered in our database.

4.4. Relative Importance of Various Stimuli in the Gregarization Process. The low densities from which the first transformation phase signs were noted in the Red locust raise questions about the nature of the stimuli involved. Progress has been made in recent years towards understanding the stimuli associated with crowding that evoke gregarious-phase characteristics in *S. gregaria*. The main focus has been on induction of gregarious behavior [5]. Simpson et al. [16, 17, 72, 75–78] have brilliantly shown in the Desert locust that mechanical stimuli appear to intervene initially; they are potent inducers of phase-transformation behavior and have a central role. The mechanoreceptors responsible are located on the outer face of the hind femur. Various authors have shown, however, especially in the Desert locust, that visual and olfactory stimuli (less active or completely inactive separately) can act synergistically and lead to both gregarious behavior and the development of black spots and yellowing of the cuticle, characteristic of gregarious hoppers [79–81]. A former experiment by Launois et al. [82],

on the Migratory locust suggests that the daily rhythm of solitary adults activity collected in the field and tested using actography near the field, can be changed depending on the density of individuals in the experimental room without any tactile contact between them, suggesting the influence of olfactory or visual stimuli in the early stages of behavioral gregarization. More recently, Simpson's group has also shown that tactile stimulation (of the antennae in this case) is necessary to induce behavioural gregarization in the Australian plague locust, *Chortoicetes terminifera* (Walker, 1870) [83]. Thus convergent behavioral responses to crowding have certainly evolved, employing different sites of sensory input according to the species.

In our case, no apparent manifestation of behavioral gregarization (coordinated movements) seems apparent in hopper populations of the Red locust at densities equal to the gregarization threshold or 10–20 hoppers/m² only, far from the hundreds of individuals in gregarious or pregregarious hopper bands. During the rainy season, the hoppers developed in homogeneous, dense vegetation covering the entire ground at an average height of 40 to 80 cm between January and March. However, the first signs of gregarization occurred at these densities, at least the pigmentary signs. The probability of tactile contact in these conditions seems relatively low. Visual, olfactory or auditory signs could also be very important in the early stages of the gregarization process when locust densities are too low (and therefore when a natural tendency for repulsion still occurs) and vegetation density is too high to allow frequent contact between individuals. Of course, in nature, mechanical, chemical, visual and auditory stimuli are all present and must act synergistically. The importance of these various factors in the induction of gregarization in the Red locust needs to be clarified in natural conditions. An excellent knowledge of the transiens phase and of its first signs is thus of fundamental interest.

Acknowledgments

Financial support was provided by the African Bank for the development, within the framework of the project for preventive locust control in Madagascar (2005 to 2009) and with a contract with the Malagasy National centre for rural development (FOFIFA). The authors are grateful to these organizations for their confidence. They also make a particular point in thanking the Malagasy National locust centre, its survey department, and all the field staff having greatly contributed to facilitate the sampling work, as well as Professor Anne-Marie Razanaohaitse, from the University of Tuléar, for her continuous support and encouragements.

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