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Desert locust gregarization: a conceptual kinetic model

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Abstract

A better understanding of the mechanisms that underlie phase transformation in a solitarious desert locust population is an important prerequisite for the development of a quantitative gregarization model and for predicting locust outbreaks. Two types of processes are involved: 1) clustering at diminishing spatial scales, which brings dispersed locusts together and which, in patchy micro-environments with a concentrated food resource, gives rise to nuclei of pheromone-emitting, gregarizing insects; and 2) recruitment processes which promote the horizontal spread of gregarious traits from such nuclei. Because of the heterogeneity of typical breeding habitats and divergent behavior of the 2 phases of the insect, there is a dynamic interplay between the forces of crowd formation and those of dispersal. All the key steps in the course of phase change are reversible and for successful development of a viable gregarious population, all must proceed at optimal pace toward the gregarious phase. The process resembles a chemical transformation that involves a series of reversible sequential steps and may, likewise, be treated as a series of equilibria. Such a conceptual model may constitute a useful framework for quantitative studies in desert locust primary breeding areas and in the development of a predictive gregarization model.

Key words

desert locust, *Schistocerca gregaria*, gregarization, clustering , recruitment, kinetic model

Introduction

Desert locust outbreaks are large-scale phenomena that evolve from concentration, multiplication and gregarization processes in solitarious populations at lower spatial scales (Roffey & Popov 1968). Although solitarious populations of the insect occupy a large zone of over 16 million km^2, only parts of this provide conditions that are favorable for sustaining outbreaks (Popov 1965, Popov *et al* 1991). Concentration and breeding occur only in areas that have received enough rains (25-30 mm), which can furnish sufficient moisture for eggs to develop and for vegetation to germinate or regenerate, to provide food and shelter for solitarious nymphs (Bennet 1976; Bashir *et al.* 1998, 2000). Within these areas, habitats differ appreciably in their capacity to support locust survival and multiplication. Solitarious locusts are known to associate with and feed on certain annual plants, which appear to perform well in habitats with certain edaphic characteristics (Maxwell-Darling 1936, 1937; Roffey & Stower 1983; Chandra 1984; Bashir *et al.* 1998, 2000; Culmsee 2002; Woldewahid 2003). Scanty and erratic rainfall in breeding areas, typically averaging between 80 and 400 mm annually, with a coefficient of variation of about 70%, means that significant breeding occurs only if there is considerable coincidence in time of rains and adult locusts in specific habitats (Rainey 1963) and this accounts for the sporadic nature of locust outbreaks (Roffey 1990).

Although suitable habitat conditions in successive breeding seasons may lead to increases in solitarious locust numbers, the probability of such populations undergoing significant phase shifts in nymphal and adult stages and developing into an outbreak cannot be reliably predicted (Dempster 1963, Roffey *et al.* 1970). Approaches based on large-scale population dynamics, that do not take into account local events and circumstances associated with phase dynamics (the key to locust transformation into a formidable migratory pest), have not met with noteworthy success (Launois *et al.* 1992, Despland *et al.* 2000). Thus, a better understanding of the mechanisms that underlie phase transformation in a locust population is an important prerequisite for predicting locust outbreaks.

Considerable progress has been made since the last plague, occurring in the second half of the 1980s, in elucidating the processes involved in the genesis and evolution of a gregarious population. In this paper, we first outline these processes and the roles they may play in the course of gregarization. We then propose their synthesis into a conceptual gregarization model, which could guide semifield and field studies and lead to a quantitative description of the gregarization process.

Processes associated with gregarization

A series of insights arising from desert locust behavioral, ecological and chemical ecological studies during the last 15 y are helping to unravel the mechanisms that underlie the transformation of solitarious individuals into dense, gregarious populations. Two types of processes may be distinguished: clustering effects, which bring dispersed locusts together and which, in appropriate micro-environments, may result in the formation of gregarizing groups; and recruitment processes, which promote area-wide spatial and temporal spread of gregarious traits from such groups.

Clustering processes.— These operate at several diminishing spatial scales. On the largest scale, distribution of solitarious locusts is markedly seasonal, dependent upon rainfall patterns and facilitated by long-distance downwind migration of the insects towards areas of horizontal wind convergence, where there is high probability of encountering rains (Rainey 1951). During the dry season, locusts do not mature. Interestingly, the majority of females that arrive in a potential breeding area at the onset of rains have been found to have mated in the previous season (Ould Ely 2003), although this needs to be confirmed in diverse breeding seasons and areas. Maturation coincides with the bud burst and emission of volatile terpenoids from certain desert shrubs, just before the onset of the rainy season 1 or 2 wk before the appearance of the annual vegetation (Carlisle *et al.* 1965, Carlisle & Ellis 1967, Assad *et al.* 1997). Maturation ensures that locusts are retained in such areas and breed there.

Within breeding areas, solitarious adults show preferences for habitats with a certain composition of plant species. In a detailed survey of egg pods laid by solitarious females at the onset of 3 successive winter-breeding seasons in the Red Sea area near Port Sudan, Bashir *et al.* (2000) found about 66% of the pods adjacent to *Heliotropium* spp. and about 32% near bulrush millet, *Pennisetum americanum*, with the rest of about 50 plant species accounting for only 2%. Large proportions of solitarious nymphs that emerged fed or roosted on these plants (~60% on *Heliotropium* spp. and ~26% on *P. americanum*). Volatile kairomone emissions from such plants may facilitate recognition and location by solitarious locusts (Haskell *et al.* 1962). A laboratory study shows desert locust survival and fecundity to be higher on these plants than on 27 other potential plant food species that occur at the Red Sea coast (Abdel Rahman 1999).

A recent study has confirmed strong preference by solitarious locusts for habitats dominated by the *Heliotropium*/millet community on the Red Sea coast (Woldewahid 2003). Significantly, these habitats are characterized by fine, sandy soil, with better moisture retention (which facilitates development of the eggs) and higher floral nitrogen content. Elsewhere in the desert locust recession areas, where *Heliotropium* spp. are a minor part of the desert flora, other plants, such as *Schouwi*a, *Tribulus* and *Depterigium* spp., may play a similar ecophysiological role (Bashir *et al* 2000). Large fluctuations occur in the distribution pattern and density of such plants, as well as in solitarious locust numbers that arrive at these areas in different breeding seasons. Habitat heterogeneity characterized by the presence of patchy distribution or low densities of the plants may provide active micro-environments for small-scale forced crowding of otherwise reluctant solitarious hoppers. The resultant repeated mutual mechanical and chemotactile stimulations of individuals in the crowd, induce shifts in individuals to the gregarious phase that is manifest in behavioral change and in the emission of cohesion (aggregation) pheromone (Roffey & Popov 1968, Bouaïchi *et al.* 1996, Deng *et al.* 1996, Heifetz *et al.* 1996, Collett *et al.* 1998, Bashir *et al.* 1998, Hassanali *et al.* 2005).

Recruitment processes.— At the onset of gregarization in a given breeding habitat, numerically dominant numbers of solitary individuals that avoid one another co-occur with small groups of gregarizing insects in restricted micro-environments (Roffey & Popov 1968, Roffey *et al.* 1970). Field observations and laboratory studies have led to the identification of 3 principal recruitment processes that may, under appropriate conditions, facilitate rapid horizontal transfer of phase characters across the population.

First, sensory and behavioral responses of solitarious adult locusts to the gregarious-phase cohesion pheromone have shown, that although this phase of the insect does not produce cues affecting behavioral clumping of individuals, immediate responses of solitarious individuals to the gregarious-phase pheromone and its components, are comparable to those of their gregarious counterparts (Njagi *et al.* 1996). The results indicate that solitarious insects that encounter pheromone-emitting nuclei of gregarizing locust groups will be arrested and recruited into these groups. Locusts that are crowded after generations of solitary-rearing conditions have been found to exhibit more pronounced gregarious characters, such as locomotor activity (Michel 1980) and levels of pheromone emission (Deng *et al.* 1996), than their continuously crowd-reared counterparts, and may thus be particularly effective in drawing solitary insects into the crowd. In the field, solitarious nymphs are often seen to join hopper bands and previously solitary-living adults seen to depart with gregarious adults leaving overnight roosting sites (Roffey & Popov 1968).

Second, in breeding habitats, mixed-phase pairs of gregarious males and solitarious females are a relatively common sight (Ould Ely *et al.* 2006). A detailed study in the laboratory that compared the mate-location responses of solitary-reared males and similarly reared males that had been crowded for varying periods, has shown that males that had experienced crowding were significantly more successful in locating solitary-reared females than their solitary counterparts (Ould Ely *et al.* 2006). Likewise, females that had been crowded, responded more strongly to solitary-reared males than did their solitary-reared female counterparts. These results indicate that gregarising males and females actively seek out and mate with their solitarious counterparts, and thereby facilitate their recruitment into the gregarizing population.

Third, gravid solitarious females switch their oviposition choice from the vicinity of preferred desert plants to the vicinity of gregarious egg pods, when these are present (Bashir *et al* 2000). Gregarious and gregarizing females prefer to lay their eggs communally, in open ground, away from plants (Popov 1965). This is mediated in part by volatile chemical constituents present in the egg froth or excreted into the sand by ovipositing females (Saini *et al.* 1995, Rai *et al.* 1997, Torto *et al.* 1999). This behavior ensures high egg pod densities at oviposition sites and resultant spatial cohesiveness of the progeny (Norris 1970, Bashir *et al.* 2000). A factor secreted into soil by ovipositing females has been shown also to prime the shift of developing embryos to the gregarious phase and to facilitate trans-generational transfer of gregarious traits to the progeny (Pener 1991; Islam *et al.* 1994ab; Bouaïchi *et al.* 1995; McCaffery *et al.* 1998; Malual *et al.* 2001). Thus, the shift in oviposition preference of solitarious females in the presence of egg pods derived from gregarious/gregarizing females, represents another mechanism of recruiting the solitarious phase into a gregarizing population (Bashir *et al.* 2000).

Locust gregarization: a conceptual kinetic model

The previous outline of the mechanisms involved in the course of locust gregarization suggests the following key sequential steps in the process:

(i) arrival, maturation and reproductive activity of solitarious adults in a preferred breeding habitat;

(ii) expression of oviposition preferences by solitarious females, food preferences of solitarious nymphs, and forced crowding of the nymphs into relatively isolated micro-environments, leading to the formation of nuclei of gregarizing hoppers;

iii) a 'snowball' effect arising from these nuclei through recruitment of solitary nymphs at first and successive instars until members of the last instar fledge into adults; and

(iv) multiple recruitment processes (involving arrestment of solitarious individuals by pheromone-producing gregarizing groups and their enlistment, preferential mating by gregarizing males and females with their *solitaria* counterparts, and preferential attraction of ovipositing *solitaria* to clusters of *gregaria* egg pods) occurring within and beyond the primary breeding habitats, together with higher mobility of adults, facilitate the spatial spread of gregarious traits and development of a gregarious adult population.

Successful development of a viable gregarious population in a habitat, within a typical breeding season, means that each of the above steps must proceed at an optimal pace and to an optimal extent. In a gregarizing population there is a dynamic interplay between the forces of dispersal and those of crowd-formation (Roffey & Popov 1968, Roffey *et al.* 1970). Each of the key steps may proceed in either direction, depending upon habitat vegetation structure and intensity (which is dependent on levels and pattern of precipitation) and the initial numbers of solitarious adults that arrive in the habitat, their reproductive success, and survival. The process may be depicted as a series of equilibria as illustrated in Fig. 1.

The scheme shown in Fig. 1 resembles a sequential series of chemical reactions (although there are clearly major differences) and provides an opportunity to treat the habitat-wide gregarization process quantitatively. Its implication is that the phase status of a population is dependent on the rates of the forward processes, relative to rates of the reverse ones. For example, seasonal precipitation may be too scanty to sustain optimum development of eggs laid by solitarious adults and/or the growth of the preferred annual plants that provide food for nymphs that emerge. Or, precipitation may be average, but the number of solitarious adults that arrive at the habitat initially is too small to provide a sizable hopper generation. In such situations, the rates of the forward gregarization processes are likely to be slower than those of the reverse processes that keep the insect largely solitarious.

Alternatively, rainfall may be relatively heavy and support a rich and spatially uniform growth of vegetation. In such a situation, dispersal of nymphs, of an average population density, is likely to proceed faster than localized clustering, and no significant phase change can occur (although such a situation may contribute to increases in the number of solitarious locusts). Significant shift toward the gregarious phase can occur only when solitary locust numbers, precipitation and resulting vegetation structure, attain certain optima. Quantification of the overall rates of phase change under different combinations of solitarious numbers, plant distribution structure and density, is expected to provide an estimate of the probability of the emergence of a viable gregarious population.

Implications of the kinetic model for further studies

This kinetic gregarization model provides a conceptual framework for field studies in locust primary breeding areas that could lead to the development of a predictive gregarization model. We have initiated 2 complementary sets of studies:

(i) field arena studies involving different compositions, densities, and distribution patterns of selected desert plants (comprising both those preferred and those not preferred for oviposition, feeding, and roosting by *solitaria*) and different numbers of egg pods, placed by solitarious adults (to provide different densities of solitarious nymphs), designed to monitor the rate and extent of gregarization;

(ii) area-wide aerial and ground surveys in successive breeding seasons in selected habitats, to document the relation between rainfall patterns, spatial plant community structures, solitarious insect densities, and any temporal changes in the phase status of the locust population.

The results of different aspects of these studies will be reported elsewhere.

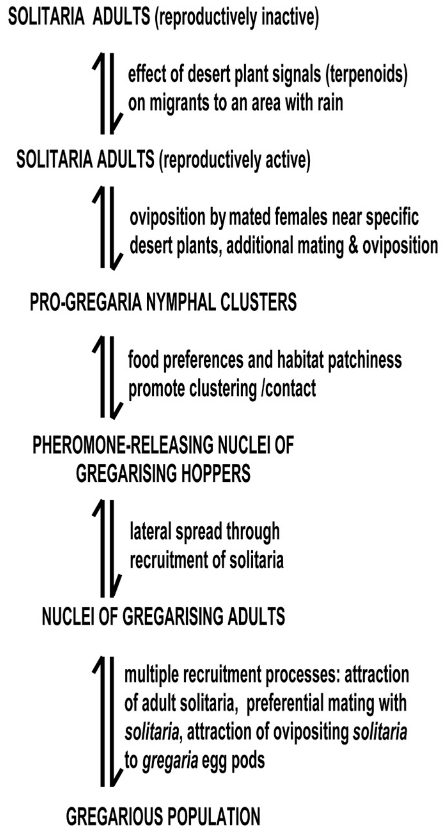

Fig. 1. Locust gregarisation: a kinetic model.

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