MINI REVIEW

Preventing desert locust plagues: optimizing management interventions

Arnold van Huis[1]*, Keith Cressman[2] & Joyce I. Magor[3]

[1]*Laboratory of Entomology, Wageningen University, PO Box 8031, 6700 EH Wageningen, The Netherlands,*
[2]*Desert Locust Information Service, FAO/AGP, Via delle Terme di Caracalla, 00100 Rome, Italy, and*
[3]*Natural Resources Institute, Greenwich University, Central Avenue, Chatham Maritime ME4 4TB, UK*

Abstract

Solitarious desert locusts, *Schistocerca gregaria* (Forskål) (Orthoptera: Acrididae), inhabit the central, arid, and semi-arid parts of the species' invasion area in Africa, the Middle East, and South-West Asia. Their annual migration circuit takes them downwind to breed sequentially where winter, spring, and summer rains fall. In many years, sparse and erratic seasonal rains support phase change and local outbreaks at only a few sites. Less frequently, seasonal rains are widespread, frequent, heavy, and long lasting, and many contemporaneous outbreaks occur. When such seasonal rains fall sequentially, populations develop into an upsurge and eventually into a plague unless checked by drought, migration to hostile habitats, or effective control. Increases in the proportion of gregarious populations as the plague develops alter the effectiveness of control. As an upsurge starts, only a minority of locusts is aggregated into treatable targets and spraying them leaves sufficient unsprayed individuals to continue the upsurge. Spraying all individuals scattered within an entire infested zone is arguably both financially and environmentally unacceptable. More of the population gregarizes and forms sprayable targets after each successive season of good rains and successful breeding. Eventually, unless the rains fail, the entire upsurge population becomes aggregated at high densities so that the infested area diminishes and a plague begins. These populations must continue to increase numerically and spread geographically to achieve peak plague levels, a stage last reached in the 1950s. Effective control, aided by poor rains, accompanied each subsequent late upsurge and early plague stage and all declined rapidly. The control strategy aims to reduce populations to prevent plagues and damage to crops and grazing. Differing opinions on the optimum stage to interrupt pre-plague breeding sequences are reviewed.

Introduction

Uvarov (1921, 1937) proposed the phase theory to explain the origin and decline of locust plagues, 6 years after he had observed migratory locusts (*Locusta migratoria migratoria*, L.) (Orthoptera: Acrididae), whose numbers were reduced by control in the Caucasus, develop into a form previously thought to be a solitary-living grasshopper. Uvarov postulated that phase change occurred in all locusts, having learned of comparable transformation in *Locusta pardalina* (Walker) in South Africa (Faure, 1923). He assumed that the associated changes in behaviour, physiology, colour, and shape were responses to population density that occurred within geographically restricted outbreak areas. Finally, he proposed that plagues start when swarms escape from outbreak areas and breed successfully in the invasion area. Consequently, a strategy of controlling incipient swarms in outbreak areas would prevent plagues.

In the late 1920s, plagues of three locusts, the desert locust [*Schistocerca gregaria* (Forskål)], the red locust [*Nomadacris septemfasciata* (Serville)], and the African migratory locust [*Locusta migratoria migratorioides* (Reiche and Fairmaire)] (all three Orthoptera: Acrididae) occurred. This focused international attention on identifying outbreak areas and developing and applying effective control, first to end the plagues, and then to prevent them. Uvarov (1951)

*Correspondence: Arnold van Huis, Laboratory of Entomology, Wageningen University, PO Box 8031, 6700 EH Wageningen, The Netherlands. E-mail: arnold.vanhuis@wur.nl

summarized field, laboratory, and cartographical studies on locusts and their control that were discussed at a series of international anti-locust conferences (Rome, 1931; Paris, 1932; London, 1934; Cairo, 1937; Brussels, 1938). Uvarov, who was receiving, mapping, and analysing a regular flow of information on current and past infestations from affected countries, described the course of these plagues, their declines, and the subsequent recessions (Uvarov, 1933a,b, 1934, 1935; Uvarov & Milnthorpe, 1937a,b, 1939).

Lean (1931, 1936) established that the outbreak area of the African migratory locust was in the flood plains of the Middle Niger River in Mali, which was then mapped by Zolotarevsky and others (Zolotarevsky, 1934, 1938; UK delegation, 1937a). The French government subsequently proposed an international supervisory system (Brussels, 1938: 320–323), and French teams supervised the outbreak area from 1938 until the convention for an international control organization was drafted in 1948. For the red locust, Allan (1931), Harris (1933), and Rosenberg (1999) identified outbreak areas, which the UK delegation proposed be supervised internationally to prevent plagues (Brussels, 1938: 307–310). The UK and Belgium supported a Red Locust Organisation from 1941 until the convention establishing an international control organization was drafted and ratified in 1950.

Developing a scheme for preventing desert locust plagues proved more problematic. Uvarov (1923) provided evidence that desert locusts change phase and phase transformation was soon observed in the field (Johnston, 1926a,b). In the 1930s, entomologists identified gregarization zones, then assumed to be permanently infested sources of desert locust plagues, in countries along the Red Sea coasts (Johnston, 1926a,b; Maxwell-Darling, 1936, 1937; Hussein, 1938), in Pakistan and India (Rao, 1937b, 1942, 1960), in Algeria (Volkhonsky & Volkhonsky, 1939), and suspected that others existed (UK delegation, 1937b). Meanwhile, cartographical analyses revealed that swarms migrate between geographically distinct winter, spring, and summer breeding zones that were often administratively separate (Uvarov, 1933a,b, 1934, 1935). Rao (1937a, 1942, 1960) subsequently established that solitarious adults also migrate between seasonal breeding areas, indicating that the desert locust, unlike the red and migratory locusts, has no permanently infested outbreak area(s). Migration and population developments were found to occur more frequently within than between three major subdivisions, the eastern, central, and western regions (UK delegation, 1938; Waloff, 1966) each of which contained complementary breeding areas activated by either winter, spring, or summer rains. A scheme to permanently supervise desert locust gregarization areas in the central and eastern regions was mooted in Cairo (Cairo, 1937) and approved, in principle, at the next Locust

Conference (UK delegation, 1938). The associated resolution urged swift action as the recession was ending (Brussels 1938, Resolution 10: 67). Funds to implement the scheme and suppress the incipient plague were not forthcoming and two plagues (1940–1948 and 1950–1963) occurred before plague prevention strategies could be tested.

The successful implementation of desert locust plague prevention requires solutions to three problems: (i) establishing the dynamics of pre-plague populations, (ii) designing a plague prevention scheme acceptable to all affected countries, and (iii) having funds and infrastructure consistent with monitoring recession populations and mounting plague prevention campaigns. We review desert locust population dynamics and the evolution of plague prevention strategies in their historical context before outlining differing views on the efficacy of control at key stages in plague development. Differences of opinion on the optimum time for management interventions are discussed, as are ways towards resolving these key policy issues.

Defining outbreaks, upsurges, and plagues

A problem faced in writing this historical review is that desert locust terminology is descriptive and it changes as knowledge of the pest's plague dynamics evolves. Some changes became appropriate when the Food and Agriculture Organization (FAO) of the United Nations formally accepted that desert locust plagues do not originate within permanent outbreak areas (FAO, 1956). Experts recommended abandoning the term outbreak, which was initially used to describe plagues and later to describe their onset. They also recommended that 'gregarization areas' be used instead of 'outbreak areas' for zones where the transformation of *solitaria* into *gregaria* occurred. A redefinition of 'outbreak' arose to describe gregarizing populations as cited below. As a result, the term 'outbreak areas', with its implications of classical plague prevention, remained in general use. The term 'recession' for interplague periods came into general use at that time but owing to the recent increased concentration on pre-plague populations, now tends to be restricted to years with few gregarious populations.

The following descriptive definitions are in general use and were derived from those in Waloff (1966, 1976), FAO (1980, 2001d), and van Huis (1994).

- **Recessions** are periods without widespread and heavy swarm infestations during which the species reverts to *transiens* and solitarious phases. Reports of swarming populations mostly refer to small and often transitory assemblages of adults or small hopper infestations. Recessions may be regional. In major recessions, sometimes called 'deep recessions', swarming populations disappear from all three regions.
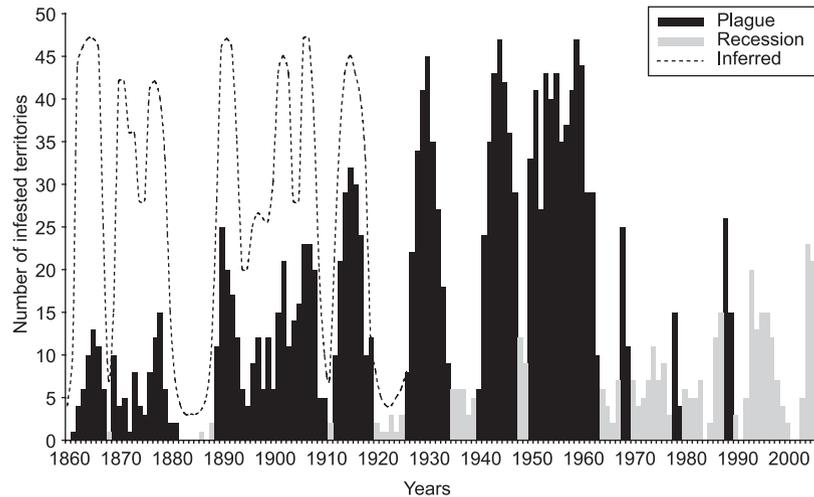
Figure 1 Territories infested by *Schistocerca gregaria* swarms during plagues and recessions 1860–2005 (modified after Waloff, 1976).

- **Outbreaks** occur when concentration and multiplication cause a marked increase in locust numbers and densities so that individuals gregarize and unless checked form hopper bands and/or swarms.
- **Upsurges** are periods in which a widespread and very large increase in locust numbers initiates contemporaneous outbreaks followed by two or more successive seasons of *transiens*-to-gregarious breeding that occupies an expanding area in complementary breeding areas in the same or neighbouring desert locust regions.
- **Plagues** occur when widespread infestations of swarms and hopper bands affect extensive areas and generate large numbers of reports during the same year and in each of several successive years (Waloff, 1966, 1976) or in one or more years (FAO, 2001a,d).

  Outbreaks (initial gregarizations) are preceded by local or general population increases occurring in non-swarming populations for one or more generations. Another frequent pre-outbreak observation is that of higher than normal numbers of solitarious immigrants (Waloff, 1966). This latter observation suggests that population increases in complementary breeding areas are involved. Analysts (Waloff, 1966; Roffey et al., 1970; Bennett, 1976) all emphasize the distinction between 'local outbreaks' and the more numerous and widespread 'contemporaneous ones' that initiate upsurges. This ambiguity in contemporary terminology exemplifies Waloff's (1966) warning to regard desert locust definitions as provisional in the absence of quantitative values for recession and plague fluctuations. The indices available then, and now, are incompletely reported changes in the extent of affected areas and numbers of sightings in them. Several of Waloff's provisional definitions (1966, 1976) reveal additional complications because they are based on information from different sections of complementary breeding areas over a period of

one or more years. Such terms can be assigned only retrospectively and when the history of events over a wide area can be reconstructed plausibly.

In this review, 'gregarization area or zone' replaces 'outbreak area', retaining the latter term for those areas within which incipient plagues of species such as the red and migratory locusts develop. The terms incipient plague and plague replace the original meanings for outbreak, which is retained for both 'local outbreaks' and the more widespread, numerous, and contemporaneous ones present at the beginning of upsurges.

Population dynamics

An examination of historical data shows that desert locust plagues were present in 4 out of every 5 years from 1860 to the end of the 1949–1963 plague and that recessions predominated subsequently (Figure 1). No regularity was found in the intervals between the onsets of successive plagues, which fluctuated irregularly in all regions (Waloff, 1976). The relative roles of drier weather and improved control measures in reducing the frequency of plague years and duration require clarification so that an appropriate control strategy and management interventions can be developed.

Waloff (1966) placed 'outbreaks' and 'upsurges', successive stages in plague development, within the major category 'recession'. Recently, Symmons & Cressman (in FAO, 2001a: 37) restricted the term recession to years with few or no outbreaks and classified years from 1860 to 2000 into 'recessions, upsurges, plagues, and declines'. Their table shows that plagues lasted longer before than after 1964 and that not all upsurges after 1970 developed into plagues. This terminology has the advantage of separating local outbreaks from upsurges but the inability to define boundaries between terms remains.

Table 1 Desert locust, *Schistocerca gregaria*, plagues and recessions 1920–2005

| | Outbreaks and upsurges during recessions | | | Plagues | | |
Recessions	Western region	Central region	Eastern region	Spread	Peak years	Decline
1920–1925	1922–1923		1922–1923			
	1925	1925	1925	1926–1927	1928–1931	1932–1934
1934–1939	1935	1934–1935	1935			
		1936–1938				
	1939–1940	1938–1939		1940–1941	1942–1945	1946–1948
1948–1949		1948	1948	1949–1950	1951–1959	1960–1963
1964–1966			1964			
	1967	1966–1967		1968	none	1968–1969
1971–1977	1974	1972–1973	1973–1974			
	1977		invaded 1978	**1978**	none	**1978–1979**
1980–1987	1980		1983			
	1985–1986	1985–1987	1986	1987–1988	none	1988–1989
1989–2002	1993–1994	1992–1994	invaded 1993			
	1994–1997	1994–1996				
		1996–1998	1997			
2003–2004	2003–2004	2003–2004		**2004**	none	**2004–2005**
		invaded 2004				

Items in bold font denote that FAO continued to use the term upsurge for these periods.

Table 1 shows the years 1920–2005 divided into recession and plague periods using Waloff's subdivisions, which were also used to produce the histogram (Figure 1) and to map recession and invasion areas (Figure 2). Upsurges were listed for each region and a pragmatic approach proved necessary to identify pre-1964 upsurges from Waloff's text because data collection was neither systematic nor regular before the 1930s and did not start in many key recession countries until the 1940s or later. In addition, routine monitoring of recession populations did not begin until the 1960s. The table clearly shows that regional recessions persist while neighbouring regions contain asynchronous upsurges, plague onsets, and declines. Finally, the table indicates an absence of peak plague years after 1964.

Waloff (1966) provisionally designated swarming populations as significant where, during an upsurge, they were
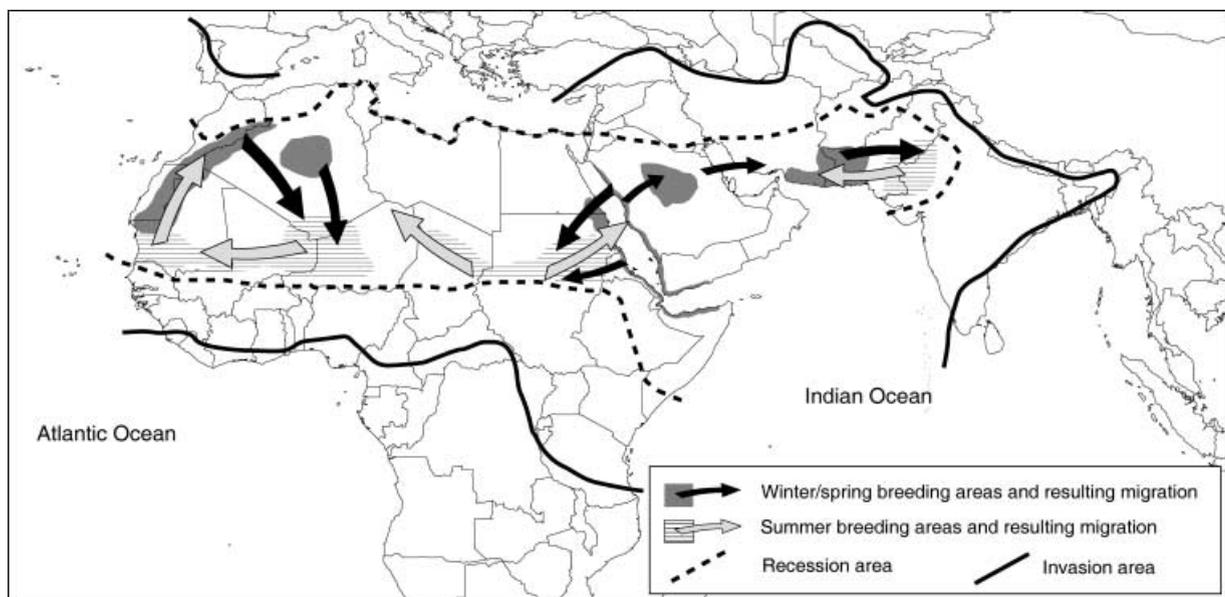
Figure 2 Desert locust recession and invasion areas with recession migration circuits (modified after Symmons & Cressman in FAO, 2001a).

sufficiently large and stable to reach the next complementary breeding area and breed as swarms, giving rise to similar or larger populations, which continued to expand the area involved. 'Plague upsurges', the stage when almost all infestations were gregarious, merges with this author's plague cycle, which she subdivided into three stages: plague upsurge and geographical spread; fully developed plague; and plague decline. The first of these stages equates with the definition of an incipient plague.

Waloff (1966, 1976) concluded that a degree of autonomy between regions caused the asynchronous onset and decline of plagues between regions. Events after 1964 confirm this view and suggest that inter-regional migration is not a feature of the very early stages of an upsurge. An important feature of plague dynamics is that weather and/or control may reverse the direction of population change at any stage in the continuum from deep recession to major plague (FAO, 2001a).

As a plague develops, the population structure varies from being mostly solitarious through an increasingly gregarious period, in which life stages are asynchronous to a final period of synchronized, gregarious infestations. Nevertheless, the boundaries between terms remain subjective and imprecise so that one person's outbreak may be another person's early upsurge; the same uncertainty exists between late upsurges and early plagues as well as between plague declines and the onset of recessions.

Phase change

Desert locusts change phase in response to rises and falls in population density, with the threshold varying according to vegetation structure and the ground cover it provides (Guichard, 1955; Roffey & Popov, 1968). Johnston (1926a,b) was the first to verify phase change among field populations when he saw the transformation in a local outbreak that was ended by control. Uvarov called the grasshopper-like form phase *solitaria* (solitarious phase) and the swarming form phase *gregaria* (gregarious phase). Intermediate forms were phase *transiens* (transient phase) and were called *congregans* (congregating) or *dissocians* (dissociating) according to the direction of phase transformation. Interpreting phase characters proved difficult in practice.

Care is needed when describing or mapping locust phases as the three frequently measured facets of phase, namely, behaviour, colour, and shape, do not change simultaneously. Behaviour changes very rapidly, and colour and shape more slowly as locusts change from phase *solitaria* to *gregaria*. Gregarious behaviour may be fully expressed after one generation of crowding in field populations, whereas changes in morphology apparently require at least three successive crowded generations to occur. In contrast, as populations dissociate, morphology changes

rapidly and behaviour alters more slowly. As a result, populations occur that behave as swarms but have morphological characters close to those considered typical of phase *solitaria*.

In addition, temperature during breeding modifies morphometrics. Gregarious hoppers developed at high temperatures had morphometrics similar to those of solitarious locusts developed at low temperatures (Stower et al., 1960), so that individual solitariform locusts need not have been low-density hoppers although gregariform adults almost certainly occurred at high densities as hoppers. Solitariform swarms may arise in two ways: from gregarious hoppers bred at high temperatures or by initially solitary adults being concentrated as adults.

Simpson et al. (1999) reviewed and clarified both the process of gregarization in the desert locust and the effect of different distributions of sparse vegetation on the rate of phase change. They selected behaviour to analyse phase change in a series of laboratory and field experiments because it represents the first visible sign of change, occurs rapidly in response to population density, and unlike colour and shape can be monitored continuously. In addition, they argued that behaviour provides positive feedbacks that drive change towards one or other extreme, and allows underlying physiological mechanisms to be correlated with a high degree of temporal resolution.

Individuals reared in isolation acquired gregarious behaviour rapidly and 4−8 h after crowding, their behaviour was indistinguishable from those of crowd-reared, gregarious locusts. Only tactile stimulation applied alone caused gregarization. The sight and smell of other locusts applied singly was ineffective but elicited gregarious behaviour in combination. Tactile stimulation was associated with mechanically stimulating the hind femur (Simpson et al., 2001), which was found later to initiate neuronal and biochemical changes that underlie phase change (Rodgers et al., 2005). Females determine the phase (behaviour and colour) of their offspring, according to the extent and recency of their own crowding and the phase of their mate, by adding a water-soluble chemical agent from their reproductive accessory glands into the foam surrounding the eggs they lay (McCaffery et al., 1998; Malual et al., 2001).

Behavioural solitarization varied with the duration of crowding that preceded isolation. Isolated locusts, crowded for 24- or 48 h and then re-isolated, lost their gregarious behaviour as rapidly as it was gained. In contrast, when crowd-reared nymphs were isolated, they partly solitarized in the first hour but required isolation over several stadia before further solitarization occurred. The ability to gregarize and solitarize offspring as late as egg laying and differences in dissociation with crowding history explain the sudden onset and slower end to gregarious populations in the field.

Concentration, multiplication, and gregarization

Three inter-related and overlapping processes precede phase change, concentration, multiplication, and gregarization (Kennedy, 1939; Roffey & Popov, 1968). Roffey and Popov's observations occurred in one of a sequence of gregarization sites and some antecedents of their populations had been gregarized for part of their lives.

Airborne concentration. The exact role that low-level wind-field convergence plays in gregarization has yet to be established. We concur with Waloff (1966: 84–87), who, considering gregarization between 1925 and 1964, concluded that concentrating scattered locusts into areas of rainfall where multiplication could occur and the progeny gregarize is potentially more important for the gregarization process than the initial increase in density. Nevertheless, on some occasions, airborne-scattered locusts may be concentrated sufficiently for swarms to form as the following authors suggested (Rao, 1942; Cochemé, 1966; Varma & Sharma, 1966; Skaf, 1978) rather than only sufficiently for the progeny to gregarize as others suggested (Rainey, 1951; Bhatia, 1961; Popov, 1968; Bennett, 1976). Rainey (1965) postulated convergence on a wide geographical scale when he suggested that convergent windfields flowing into a tropical cyclone in late October 1949 concentrated locusts from surrounding countries into the parts of Oman made suitable for breeding by the associated heavy rains. The outbreak seen subsequently was one of several in the central and eastern regions that marked the onset of the 1949–1950 plague upsurge. Popov (1968) and Bennett (1976) deduced a similar role for a cyclone in Oman as the 1968 plague upsurge was beginning. Rainey (1965) interpreting events during a particularly short recession, speculated that swarms from the previous plague (1940–1948), last seen 3 months earlier in Eritrea and 6 months earlier in Baluchistan, provided evidence of swarm continuity between plagues, the plague continuity hypothesis discussed in a later section.

Alternative interpretations of airborne concentration on population processes occur because incomplete data are being analysed and because the convergence known to exist around storms and cyclones may be interpreted as a direct cause of gregarization when in fact multiplication on associated rains was involved. Only Cochemé (1966) demonstrated that the horizontal windfield convergence was sufficient to concentrate scattered locusts into a swarm. Venkatesh (1971), using Cochemé's methods, re-examined and rejected Varma & Sharma's (1966) inference of swarm formation for two reasons. First, the convergence associated with the cyclone would not have increased the density of airborne particles (locusts) sufficiently, and second, the cyclone's windfields did not pass over sources of scattered

locusts, whereas those of westerly winds from Pakistan did. Instead he deduced it more probable that the swarm and scattered locusts were transported on westerly winds from sources in Pakistan and then bred in areas of green vegetation initiated by rainfall linked to the cyclone.

Concentration into habitats. The first process observed by Roffey & Popov (1968) was 'large-scale concentration' of an estimated 5 million solitarious immigrants, originating tens or hundreds of kilometres to the south into areas of green annual vegetation, particularly the *Tribulus* and *Schouwia* habitats, that occupied less than 10% of their 2.5 million ha study area. This led to observed adult densities (100–2000 per ha) being 50–100 times greater than if the locusts had been uniformly distributed. Further concentration within the preferred habitat occurred during breeding as males searched for females and the latter sought oviposition sites. Densities at some oviposition sites reached levels comparable to those in swarms. In fact, reports of groups or swarmlets laying are frequently the first indication that gregarization is in progress. Hatching densities and hopper interactions affected the rate of gregarization. Hopper interactions were affected by weather and the ground cover (composition, size, and structure) provided by vegetation. Finally, as the season ended, vegetation began to dry out and locusts concentrated into areas that remained green.

Multiplication. Little quantitative information exists on increases in numbers that precede phase change and no global estimates for the numbers in recession populations that show no gregarious behaviour were found. The spacing between individuals tends to be large (Roffey, 1965) and indicative densities for mapping are set at <25 per ha, a value derived from surveyors seeing a single locust during a transect sampling a 400-m^2 area.

Very rough numerical estimates exist for a few non-gregarious infestations but it is often difficult to discern their phase and the proportion of the seasonal population they represent. Roffey (1965) considered that $10–10^9$ individuals in a population, not itself markedly gregarious, could give rise to high-density populations of swarms and bands under suitable ecological conditions and that numbers need to rise to 10^{11} to represent populations typical of those during plagues. He derived these values in part using unpublished studies by Stower recording similarly behaving populations, ranging from 1.1×10^3 to 1.5×10^8 at mean densities of 0.23–0.95 per m^2. Roffey suggests that areas for such populations are likely to vary from 10^3 to 10^5 km^2, and cites the Rajasthan Desert, Darfur, and Kordofan in the Sudan and the central Sahara as typical localities. This indicates that he was referring to populations found

within major parts of seasonal breeding areas in all three regions. He concluded that the essential difference between populations in which gregarious behaviour is poorly developed, and gregarious ones, lies not so much in absolute numbers but in the degree to which the individuals are concentrated. The fact that subregional populations of 10^8 individuals occur with poorly developed gregarious behaviour makes the threat of a plague very real if control is ineffective.

FAO (2003) contains known examples of multiplication rates. Those leading to local outbreaks or upsurges, cited here, relate to subregional populations. Stower (1962) emphasized that the significance of an outbreak varies with the numbers of individuals changing phase. Thus, phase change in populations as small as 10^3 individuals is of little significance in swarm formation. Whereas, initially small populations that breed successfully and rapidly for a number of successive generations may reach dangerous levels. He cited the estimated 1000-fold increase over three generations from 2.5×10^5 to 2.5×10^8 locusts observed breeding over a 6-month period on the Red Sea coast as a plague upsurge was beginning in the winter of 1948/1949.

A 10-fold increase per generation, based on such observations, became accepted as a plausible multiplication rate for reconstructing pre-gregarization developments among partially reported populations. Roffey (in Joyce, 1962b) suggested a 1000-fold multiplication in northern Somalia in the winter 1956/1957 when three generations bred and ended a regional recession during the 1950/1963 plague. Waloff (1966) conjectured that it was reasonable to infer that a scattered population numbering 2–3 million had bred twice in quick succession to achieve a 100-fold increase after heavy rains in Algeria in November 1938. This inferred population and multiplication rate accounted plausibly for the population of scattered locusts and swarms numbering an estimated 180–300 million, seen within a 60-km^2 infestation in Wadi Botha in June 1939 by Volkhonsky & Volkhonsky (1939). Popov (1968) reconstructed events, consistent with locust sightings by travellers, in Oman in the 6 months preceding swarms appearing as the 1966–1968 upsurge began. He assumed that very few locusts were present to breed after the initial rains in November 1966 and that gregarization occurred following a 10-fold multiplication for each of three subsequent generations. He also suggested that travellers seldom notice locusts until gregarization has started. The fact that routine monitoring surveys also fail to reveal the rise in numbers that precede gregarization is discussed under optimizing management interventions.

Gregarization. Roffey & Popov (1968) estimated that a 16-fold multiplication occurred between laying and the fourth

nymphal stage in Tamesna in 1967, after which control began to reduce numbers. They recognized two main patterns of gregarization even though individuals gregarized to a markedly different extent within subpopulations. In the first case, low-density hatchlings moved to nearby vegetation and remained quiescent except when moving individually to feed, or in response to diurnal changes in microclimate. Few interactions arose until densities increased to 3–5 locusts per plant, the equivalent of 5–15 per m^2 due to further hatching and habitat loss as the vegetation became dry. Interactions at these higher densities led to groups forming during roosting, basking, and feeding. Disturbance by grazing camels and high densities of grasshoppers accelerated gregarization and initiated marching, though whether directly by tactile stimulation or indirectly through concentration into ungrazed vegetation was not stated. When marching began, the hoppers were widely separated with densities of 1–2 per m^2 but with increasing age and gregarization the number and density of marching hoppers rose to 10–20 per m^2 in open ground. Finally in some areas, well-defined bands appeared.

A second pattern occurred where adult immigrant densities exceeded 1000 per ha (Roffey & Popov, 1968). These locusts formed groups and a proportion of the immigrant males acquired the yellow colouring typical of gregarious populations. This degree of adult gregarization affected the behaviour and colouring of hatchlings. Groups formed immediately in populations numbering many hundreds per square metre, whereas those at lower densities dispersed.

Despland & Simpson (2000) varied the microstructure of the experimental environment to explore the effect on the distribution of locusts, their interactions, and hence their phase status. They found that phase differences related to vegetation structure were transmitted to progeny. Plants within experimental field arenas of 2 m^2 gave approximately 13% ground cover and were distributed at low-, medium-, and high-fractal dimensions or clumping. Adults assayed after 10 days in an arena had become progressively more gregarious with increasingly clumped vegetation. Those from arenas containing clumped vegetation formed basking groups and mature males were yellow. Progeny of these locusts, laid within the arena, tested within 4 h of hatching were more gregarious than the progeny of adults kept in scattered vegetation. The colour of hoppers, however, did not show such clear-cut differences. These experiments demonstrated the importance of vegetation microstructure in desert locust gregarization over spatial scales of centimetres to a few metres but represented less ground cover than during the gregarization observed by Roffey & Popov (1968).

Most populations observed by Roffey & Popov (1968) were in *Tribulus* and *Schouwia* habitats in which the ground cover exceeded 15%. Hoppers started to group between

the second and fourth instar and showed signs of black pigmentation at densities of 5–15 per m^2. At Mbika, a site with lush vegetation, grouping occurred among hatchlings, but little marching was observed. Post-hatching densities were high, averaging 30–40 per m^2 and peaking at 500 per m^2, but the *Tribulus* provided 60% ground cover and was greener and denser than elsewhere. At sites with sparser vegetation, bands and swarms appeared among less dense subpopulations (>20 per m^2) as vegetation with a lower cover (<20%) dried out. This suggests that the vegetation mosaic in the latter but not in the former was appropriate for inducing gregarization.

The potential role of plant structure and quality as well as its distribution on locust populations needs further clarification. Popov et al. (1978) found that open, small leaved plants, like *Dipterygium glaucum* Den. (Capparidaceae) promote aggregation and gregarious characteristics, while dense leafy plants like *Chrozophora oblongifolia* (Del.) Juss. (Euphorbiaceae) are conducive to dissociation and development of solitarious characteristics. The effect is probably mechanical as sparser vegetation promotes contact.

Jackson et al. (1978) found that a diet of *Pennisetum* or sorghum (*Sorghum* spec.) (both Poaceae) tended to enhance gregarious characteristics, while *Dipterygium* accentuated solitarious characteristics. Desert locust reared on high-nitrogen millet leaves developed faster, showed greater synchronization, had a higher fecundity, and reproduced earlier than individuals fed on low-nitrogen leaves (Woldewahid, 2003). It is interesting to speculate whether a connection exists between drought breaking rains, high-nitrogen content of plants, and gregarization and outbreaks among desert locusts as was found for the African armyworm, *Spodoptera exempta* Walker (Lepidoptera: Noctuidae) (Janssen, 1993).

Plague initiation hypotheses

Gregarization areas found in the 1930s were mainly in the winter and spring breeding areas of the central and eastern regions but outbreaks associated with the two subsequent plagues confirmed indications that gregarization also occurred in the western region and in summer breeding areas. In addition, the wide distribution of solitarious desert locusts did not support the view that gregarization areas were particularly favourable for permanent habitation but that they sometimes favoured the gregarization process (Uvarov, 1951). An explanation of plague origins other than the model used for the red and migratory locusts was needed for the desert locust.

Experts meeting during the 1949–1963 plague concluded that it was no longer tenable to assume that desert locust plagues would arise in a few permanent outbreak areas and that a scheme for preventive control must await greater knowledge of the pest's plague dynamics (FAO, 1956). In addition, as a rapid examination of all available records showed that swarms had occurred in all recession years since 1887 (Figure 1, FAO, 1956; Waloff, 1966), they further concluded that it was uncertain whether plagues start with the concentration of scattered locusts followed by successful breeding and gregarization, an extension of Uvarov's phase theory, or from the carry-over of swarms during recessions, the continuity hypothesis, or from a combination of these processes (FAO, 1956, 1959, 1969). When a recession spread across the invasion area between 1960 and 1964, these hypothese were examined in more detail.

The continuity hypothesis. Rainey & Betts (1979 and in FAO, 1967) extended the continuity hypothesis and its implications for control using a series of inter-related suppositions about 'important' populations during recessions. They inferred links between these populations based on routes previously followed by swarms, a plausible but untested hypothesis. Accepting this inference allowed them to interpret links as circumstantial evidence that populations were successive samples from the same population or its progeny. Control could then be considered cumulative, in the sense that it potentially reduced the initial size of the subsequent sighting or generation.

The 'important recession populations' selected for analysis by Rainey & Betts (1979) represented a first attempt to identify infestations with the potential to initiate plagues and the control tactics able to maintain recessions (FAO, 1967). The selected populations were 53 clusters of infestations, 23 of which had been treated. They were of three types: bands and swarms, other populations that were controlled, and infestations estimated as containing 'millions of individuals'. Essentially these were the locusts, between July 1963 and September 1967, that were gregarious or might become so after breeding.

The populations selected as 'important' were not controversial. Similar populations had been controlled to prevent swarms forming since the 1920s (Johnston, 1926a,b; Waloff, 1966). Similar populations sometimes called 'dangerous' and 'notable', were used for analysing subsequent upsurges (Bennett, 1974, 1975, 1976; Karrar, 1974; Roffey, 1982). The controversial aspects of the continuity proposal were (i) an inability to provide convincing links when recession populations were at their lowest, and (ii) whether concentrating solely on 'important populations' was the best method of finding all areas of large pre-gregarization increases in locusts that precede the initiation of plagues.

Phase theory adapted. Waloff (1966) analysed the archived record of recession populations up to 1964. She established that plagues did not arise solely from gregarious populations

persisting throughout recessions and that concentration, multiplication, and gregarization were important processes contributing to the build-up of *transiens* to gregarious populations. She used the fact that locusts move seasonally between complementary breeding zones during recessions to estimate the number of generations separating populations recorded as gregarizing or gregarious during recessions from their potential gregarious progenitors. The four plague upsurges between 1920 and 1964 provided her with only one case, Oman in 1949, in which the initial *transiens* to swarming locusts might have included gregarious locusts from the previous plague. When she examined the genealogy of the 63 swarming or near-swarming populations seen during recessions between 1920 and 1964, 41% were definitely or probably the F_1 progeny of swarms, 30% were F_2, 17% were F_3, and 12% were the F_4–F_7 from swarms. Waloff also showed that recession populations are confined to the drier, central portions of the invasion area (Figure 2), and identified inter-regional migrations by recession populations during upsurges. Successful breeding requires a high degree of spatio-temporal coincidence between adult locusts and rain. This is achieved by downwind migration, which takes locusts towards areas of horizontal wind convergence where rain falls (Rainey, 1951, 1963). Weather associated with emigration from breeding areas, which may control the ultimate destination of migrants, is less well understood.

Waloff (1966) cautioned that the location of both plague and recession migration circuits differed between years because they are dependent on the sources and phase of emigrants and trajectories of locusts in the windfields during migration. The main breeding areas and migration circuits active during recessions are clearly regional (Figure 2) as they are when extended into the invasion area during plagues. Nevertheless, Waloff considered the invasion area to be a single unit because swarming populations, breeding once or more en route, are able to move across all three regions.

Roffey et al. (1970) summarising observations on the recession populations during the 1960s concluded that outbreaks, upsurges, and plagues belonged to a single continuum. Gregariously behaving populations were frequently observed in recessions but were smaller and less dense, and often dispersed unlike bands and swarms found in plagues. Waloff (1966) and Hemming et al. (1979), in disputing the continuity hypothesis, did not ignore links between populations but placed greater emphasis on concentration and multiplication leading to population growth and gregarization.

Rainfall and the plague cycle

Roffey et al. (1970) contrasted the smaller scale of rain and hence breeding habitats that precede local outbreaks with those preceding the many contemporaneous gregarizations that begin an upsurge. Sizes of areas involved cited in the literature are difficult to interpret without supplementary information on infestation type and distribution. Values are often derived from polygons drawn round infestations, whether or not the locusts were clustered and leaving large parts of the polygon uninfested. A few case studies estimate the dimensions of individual outbreaks or one among many similar neighbouring outbreaks. Values for single infestations vary between 10 ha and 20 km^2 (Varma & Sharma, 1966; Roffey, 1981). Larger areas varying from 2500 to 100 000 km^2 refer to subregional infestations belonging to upsurge sequences (Roffey & Popov, 1968, see figure 5 in Bennett, 1976; Roffey, 1982). They rise to 200 000 km^2 when rain-affected areas were estimated (Bennett, 1976).

Finally, Roffey et al. (1970) provided evidence that the low and erratic rainfall of the recession area causes many upsurges to be short lived and found that it was rare for weather to promote continuity in high-density recession populations for more than two or three generations. The exceptions occurred during upsurges that developed into plagues.

Waloff (1966), while evaluating the genealogies of recession populations noted that each migration circuit had one season (shown in italics) that failed to support breeding every year (Table 2). Good rains in these seasons appear to occur as an upsurge develops and the absence of breeding

Table 2 Seasonal pattern of *Schistocerca gregaria* in solitarious breeding (after Waloff, 1966)

Western region			Central region		
S. circuit (swarms)	*N. circuit* (swarms)	*N. circuit* (not swarms)	North of 12°N	South of 12°N	Eastern region
Summer[1]	Summer	Summer	Summer	*Summer*	Summer
		Autumn/winter	*Autumn/winter*	Short rains (winter)	*Autumn/winter*
	Spring	Spring	Spring	Long rains (Spring)	Spring

[1]Breeding not clearly demonstrated until 2005.
Season in italics denotes that breeding does not occur every year.

during these seasons seems to coincide with the end of upsurges. These impressions await rigorous testing. Her text shows, however, that poor rains in other seasons also cause breeding to fail during plague declines.

Bennett (1974, 1975, 1976) concluded that an upsurge occurs when rains are timed to reduce the risk of pre-breeding mortality among adults, and she cited two mechanisms involved here. One occurs when rains continue in source areas so that fledglings mature quickly and lay eggs without emigrating to a complementary breeding area. The other involves rains being sufficiently widespread in complementary breeding areas to enable most migrating adults to reach suitable breeding habitats when flying downwind in almost any direction. Both mechanisms operate during plague upsurge sequences.

Bennett found that a minimum of 25 mm rain was required for the ephemeral food and shelter plants of the locust to germinate and for successful breeding. She defined successful breeding as an increase in numbers from mature parents to filial fledglings because the adults frequently emigrated. Rainfall exceeding 25 mm over wide areas in winter and spring are most often associated with deep troughs in the mid- and upper tropospheric westerly winds. A higher threshold (30–35 mm) needed in summer is usually exceeded in summer breeding areas.

This valid finding on minimum rains does not capture the exceptional nature of the rains and floods that initiate upsurges and no parameter estimates yet exist to characterize such rains in each breeding zone. Waloff (1966) cited examples associated with local outbreaks. Values included 401 and 253 mm that were 5.4 and 2.7 times normal, respectively, on the Red Sea coast of Sudan in 1925. Amounts were 206 and 151 mm in the same area in the winter of 1934–1935. Pedgley & Symmons (1968) discuss the rains associated with the 1967–1968 upsurge and the map depicting rain histograms in north-eastern Africa and in Arabia shows the paucity of stations in the central region and the prevalence of incomplete datasets. Illustrative of values for that upsurge was Djibouti with 282 mm in November 1967, which was over 12 times normal. Monthly totals between 80 and 100 mm fell in all affected regions and often more than once.

The global circulation patterns involved in upsurge-promoting rains remain partially understood and no reliable quantitative estimates exist for the rains that promote high multiplication rates. Autumn and winter rains initiating upsurges are associated with global circulation patterns in the tropospheric westerlies of the Northern Hemisphere. These bring a sequence of depressions and rains to one or more desert locust regions in latitudes containing northern winter and spring breeding areas (Winstanley, 1973b; Bennett, 1976). This does not negate the importance of

cyclones in generating upsurge sequences in other areas but indicates that they are not the sole cause, as implied in some studies (Ashall, 1985; Roy, 1985).

Revised plague initiation hypothesis

It is now generally accepted that upsurges start with successive seasonal rains, in one or more desert locust regions, which are more widespread as well as being more frequent, heavier, and longer lasting than normal. The frequency of rain and the duration of the rainy season allow two and a partial third generation of locusts to breed at higher rates of multiplication than normal either because more eggs and/or greater survival occur. After one or two seasons of high population growth, many approximately synchronous outbreaks appear and an upsurge begins (FAO, 1968: 86–87). The outbreaks are usually found in several countries and often in more than one region. Many scattered adults, groups, and some swarms emigrate after each generation fledges but others stay to breed so that parts of the breeding area remain infested for much longer than normal. As a result, seasonal breeding is not only widespread but occurs simultaneously instead of sequentially in complementary breeding areas. Early upsurge populations, unless checked by poor rains or control, become more gregarious and the individual infestations more numerous until the entire upsurge population is gregarious. The high density of the aggregations at this stage causes a marked fall in the area infested, which is associated with rising locust numbers (Bennett, 1974, 1975, 1976). Subsequently, populations not checked by drought, migration to hostile habitats, effective control, or more usually a combination of these factors, continue to grow and reach first plague and then peak plague dimensions and numbers (Waloff, 1966).

Heavy, protracted rains and widespread outbreaks also preceded upsurges that ended regional recessions (Waloff, 1966; FAO, 1968: 356). Such observations and studies of non-swarming populations during the 1950–1963 plague (Stower, 1962; Stower & Greathead, 1969; Roffey & Stower, 1983) strongly suggest that non-gregarious desert locusts permanently inhabit the recession area, migrating between seasonal breeding areas, and become founding members of subsequent outbreaks when heavy rains fall. In this sense, plagues not only arise from, but may be supplemented by, populations that increase and gregarize during wet sequences of weather in the recession area.

Waloff (1966) considered the implications of her findings for predicting and preventing plagues. With others, she advocated the regular monitoring of seasonal breeding areas in recessions to locate 'important populations'. The focus of studies then shifted from establishing the origins of plagues to examining the causes of upsurges and the

effectiveness of control in preventing plagues. Bennett (1974, 1975, 1976) was the first to benefit from having a regular although still incomplete record of the distribution and characteristics of recession populations to analyse the 1967–1969 upsurge and short plague. She provided evidence to support some of the links postulated by Rainey & Betts (1979) but no one has provided links to cover gaps in continuity of postulated swarming genealogies that lasted up to 18 months (time for 4–5 successive generations) during the pre-1967 plague upsurge or for subsequent gaps that were arguably longer.

Rainey & Betts (1979) correctly indicated that gregarization areas represent seasonal halting places for migrating recession populations rather than being independent starting places for upsurges and plagues. Waloff (1966) concluded that the build-up of gregarizing populations in complementary breeding areas was more a feature of successive occurrences of temporarily favourable habitats than specific localities implied by the terms outbreak or gregarization areas. This ability to clarify and resolve some earlier disputes does not imply that sufficient is yet known to evaluate the desert locust threat accurately. To do this, we need more information about the underlying systems and rainfall triggers that promote widespread vegetation and locust population growth leading to an upsurge and a possible plague.

Plague prevention

Control infrastructure

Desert locust control strategies have national, regional, and international components coordinated by FAO that interact to achieve global meta-population management and to share costs (Elliott, 2000; Lecoq, 2001, 2003; Roy, 2001). The strategy calls for countries in the recession area where gregarization occurs to maintain permanent units to find and then monitor or control gregarizing and gregarious populations. They are also expected to undertake the initial campaigns of an upsurge while organizing regional and international support with FAO assistance when large-scale upsurge elimination campaigns prove necessary (FAO, 1985).

Anti-locust organizations take longer than locusts to mount an attack. The current plague-prevention strategy requires timely and coordinated inputs from national, regional, and international sources, each of which depends on accessing reserve funds at short notice. Plague prevention will be compromised should any single level's financing cease and not be replaced. A major constraint to timely campaigns is releasing funds to deliver supplies to national and regional teams that match the temporal and spatial mobility of desert locusts as they migrate seasonally between complementary breeding areas that may be in different regions.

Campaign managers require stable recurrent finances, not only to avoid delays accessing supplies to prevent plagues, but also to select pesticide and application equipment of their choice rather than risk receiving a variety of systems from donors. They also need financing to train reserve teams during recessions rather than during emergencies. Finally, they need to be accountable for using supplies prudently and for protecting the environment, practices not encouraged by dependency on emergency assistance. Mechanisms exist and have been adapted over time to share costs between affected countries and external donors. The latter, initially countries with responsibility for plant protection in their affected colonies, are now more numerous but have locusts as one among all other calls on their development and emergency-humanitarian aid budgets.

Control methods

The most widely used control technique remains ultra low volume (ULV) application designed to spray overlapping swaths of small droplets of a concentrated pesticide formulation on to locusts at very low dose rates. The pesticide can be sprayed directly on locust groups and small bands with hand-held sprayers if infestations are of very limited extent. Larger infestations require vehicle or aircraft-mounted sprayers, for which blocks must be demarcated to include most patches or bands in the vicinity. Demarcation techniques vary with infestation size and must be quick to apply. All methods leave some locusts outside the block, which will remain unsprayed (FAO, 2001b). The difficulty of demarcating control zones boundaries is revisited under managing upsurges and plagues. Demarcating low-density populations is discussed under optimizing management interventions.

Countries with substantial agricultural production and high value export crops are largely self-sufficient in containing the desert locust threat. They have a major economic interest in regionally effective plague prevention and are currently major financiers of this strategy (FAO, 1998). Other countries require considerable assistance during plague upsurges. External expenditure during the 1986–1989 emergency amounted to US$ 324 million, of which some 16% was spent controlling contemporary upsurges of grasshoppers and other species of locusts (Joffe, 1995). The considerable expenditure per affected country was revealed in a later economic analysis (FAO, 1998). Desert locust campaigns treated 26 million ha during this emergency, using 16 million l of liquid pesticides (ULV and emulsifiable concentrate formulations) and over 14 million kg of dust formulations (Schulten, 1990). These campaigns raised awareness of potential environmental pollution and have

led to safer pesticides and systems for environmental monitoring being developed (FAO, 1989).

Post-1989 projects demonstrated that correct application techniques during block spraying with conventional pesticides improves targeting, allows lower dose rates, and so reduces adverse side effects. Research has demonstrated the value of using spray systems linked to GPS and to differential GPS for improving track guidance and spray control in aircraft and for ground spraying. Pesticide trials also suggested that barrier spraying can be reintroduced, provided that new restrictions are adopted (FAO, 2004a). This work-efficient technique, which leaves unsprayed or lightly sprayed refuges for non-target species, was suspended while persistent products with acceptable non-target impact were found to replace dieldrin. The technique requires hoppers to march to sprayed barriers, a behaviour associated with densely aggregated bands, which may not be present in early upsurge populations. The FAO Pesticide Referee Group, who review trials submitted to them, began to list dose rates of proven efficacy for barrier treatments at their fifth meeting (FAO, 1996) and have listed dose rates for fipronil and the Insect Growth Regulators (IGRs) triflumuron and diflubenzuron since their sixth meeting (FAO, 1997). After considering a review on the environmental effects of barrier spraying with these pesticides, the group advised that the slower acting IGRs generally had lower environmental side effects than fipronil, and that the latter should be restricted to barrier treatments in non-crop areas. They stated that additional precautions should be taken if persistent side effects arose and if the same area were treated repeatedly. To facilitate this requirement, they recommended that coordinates of spray blocks be recorded and spatio-temporal spray histories of locust-infested areas be derived (FAO, 2004a).

An environmentally safer but slower acting biopesticide, Green Muscle® [Biological Control Products SA (Pty) Ltd., Ashwood, South Africa] based on a fungus, *Metarhizium anisopliae* var. *acridum* has also been developed for ULV spraying, and large-scale field trials are setting parameters for its future operational use. The product has a low non-target impact, as the fungus affects mainly locusts and grasshoppers. In addition, specialist teams are being trained to undertake environmental surveys in locust habitats in order to monitor the side effects of operational pesticide treatments and to establish the effects of different pesticides on non-target species.

These new anti-locust practices promise to deliver control that is more effective and reduce risks for operators, inhabitants, livestock, and the environment. Good field practices, once assimilated by control units, will safeguard ecologically important non-target groups such as pollinators, ants, termites, and the natural enemies of locusts.

These practices meet the needs of farmers who are increasingly adopting integrated pest management and organic methods in livestock and crop production. Ensuring the uptake of the safeguards is an important aim of the desert locust component of FAO's Emergency Prevention System (EMPRES) for transboundary animal and plant pests and diseases. During the latest emergency, teams sprayed nearly 13 million ha, costing approximately US$ 20 per ha for variable campaign costs (pesticide, aircraft contracts, per diems, fuel, vehicle maintenance, food, other provisions, and medical equipment) between October 2003 and September 2005 (C Elliott, pers. comm.). Training is required to ensure that the improved and new practices are fully implemented in future campaigns.

Managing local outbreaks

In recession years with unexceptional rains, only a few sites develop sufficient vegetation for locust numbers to increase and gregarize or form swarmlets in convergent windfields. National locust teams using ground control are permanently mandated to find and destroy such 'local outbreaks' and other 'important populations' that might gregarize after breeding. The constituent bands and swarms in such periods are smaller and less dense than those found during upsurges and plagues, and tend to disperse (Hemming et al., 1979).

Managing upsurges and plagues

Early in an upsurge, the area containing aggregated infestations, treatable by ULV spraying, increases rapidly. Symmons (2003) uses plausible work rates and estimates typical of upsurge and early plague populations to gauge the resources needed to detect and control populations at these stages of plague development using ULV spraying. In a later paper, Symmons (2004) describes a model allowing the difficulties of demarcating spray zones to be investigated. The scenarios mirror real campaigns and show that ground control teams maintained during recessions are quickly unable to find and treat all infested areas before early upsurge adults and swarms emigrate. Managers must decide when their permanently retained ground spray teams need to be reinforced with local or regional reserve teams and when to switch from ground spraying individual targets and infested blocks to introduce aerial spraying of swarms and band zones. For a number of countries, the introduction of aerial spraying requires international assistance.

An added logistical problem faced during periods of longer rains and breeding seasons is that complementary breeding areas are infested simultaneously as well as sequentially, which may limit when assistance can be offered from countries within a region. In addition, swarms migrate farther than scattered adults extending the upsurge campaigns, initially to the edge of the recession area and then

into agricultural areas in the invasion area. This takes locusts into countries where Plant Protection Departments may not have teams trained to monitor and control desert locusts and into areas of more reliable rainfall where breeding is unlikely to fail completely.

Revising the plague-prevention strategy

The recession that spread across the invasion area between 1961 and early 1964 offered opportunities for implementing the long-term policy for preventing plagues proposed in 1956 (FAO, 1956) that was formally adopted in 1969 (FAO, 1969). A review of the control strategy was then sought because the biological basis of Uvarov's original strategy (UK delegation, 1938) had changed from expecting desert locust plagues to begin in permanent outbreak areas to recognizing that they occur when rains activate a sequence of sites in seasonal breeding zones that are geographically separated. Equally, the financing and infrastructure had changed radically from using an international organization, through using regionally coordinated campaigns, to national units taking over prime responsibility for operating the control strategy. Finally, control products, techniques, and perceptions of their environmental acceptability had changed and continue to change.

The immediate objectives were to prevent a new plague from developing and to determine how plagues start. An interim policy, never rescinded, of controlling 'important' locust concentrations was recommended (FAO, 1967, see FAO, 1969, Appendix V, paragraph 21; Ashall, 1985) pending acquisition of sufficient knowledge of plague initiation to define 'important' more rigorously. Simultaneously, FAO implemented a plan to improve detection of outbreaks and to find stable financing during recessions to ensure that teams were equipped to use the latest anti-locust techniques and were able to mobilise reserves rapidly during upsurges (FAO, 1969). Longer-term objectives were to develop a plague-prevention control strategy and intervention tactics adapted to the pest's population dynamics, available control techniques, and infrastructures in the recession area.

Tactics used and investigated during the 1950–1963 plague and in the desert locust project that followed (Courshee, 1965; FAO, 1968) influenced the evolution of the plague-prevention strategy and the debate on intervention tactics. Methods devised for roughly estimating locust numbers in swarm and band infestations enabled managers to evaluate the effectiveness of plague suppression campaigns. Teams focused efforts on hopper band control to avoid massive swarm invasions that might swamp control capacity, and where possible, they attacked immature swarms held in convergence zones or against mountain barriers. These tactics minimized the population surviving

to breed and eventually reach distant major crop areas (Desert Locust Survey, 1956). By 1959, control was being delivered on a scale commensurate with the size of seasonal plague populations in the central region (Joyce, 1962a). Rainey et al. (1979) mention equally effective campaigns in the eastern region and cited papers describing similar developments within francophone Africa (Perrot, 1956; Mallamaire & Roy, 1959; Sayer & McCuaig, 1961; Besnault, 1962; Gilot, 1965) and concluded that control on this scale arguably helped end the plague.

During the same plague, teams investigated the feasibility of spraying swarms as they approached Kenya's major cropping areas from or through the Somali Peninsula. Control managers assumed then, as now, that this alternative strategy would require prohibitive numbers of aircraft to prevent crop damage (Desert Locust Survey, 1956). Research on these topics and on the effective use of pesticides continued during the 1960s. The results gained encouraged spraying dense control targets such as swarms and bands to maximize kill per unit of pesticide, to lower costs, and to protect the environment. Two factors encouraged the targeting of swarms: first, band zones are larger than the area of swarms they produce; and second, bands infest only 2–5% of such zones (Courshee, 1965, 1990; FAO, 1968; MacCuaig, 1970; Symmons, 1992). These results focused attention on the emphasis to be placed on band and swarm control.

No post-1964 upsurge has developed into a fully established plague. Four (1968–1969, 1978–1979, 1988–1989, and 2003–2005) reached Waloff's plague upsurge and spread stage and then declined rapidly. None reached the dimensions and geographical extent of those before the 1960s, which frequently invaded major cropping areas in the invasion areas of all three regions in the same year. All ended when populations were fully gregarious, rains ceased to favour maximum levels of growth and adequate control was applied. In some cases, migration to unsuitable habitats occurred. The control component arguably indicates successful plague prevention but many authors now perceive an upsurge as a failure of a strategy frequently referred to as 'preventive control', a much vaguer concept than plague prevention, which is often used as though synonymous with outbreak or upsurge prevention (Figure 3).

Contending strategies

Authors used the vaguer term 'preventive control' at a seminar on control strategies (Krall et al., 1997). Showler (1997) limited this term to an, as yet unachieved, ideal in which pre-gregarization control or outbreak prevention kills sufficient locusts to stop further developments. In the meantime, he recommended proactive control, the use of early intervention as a means of providing a flexible approach
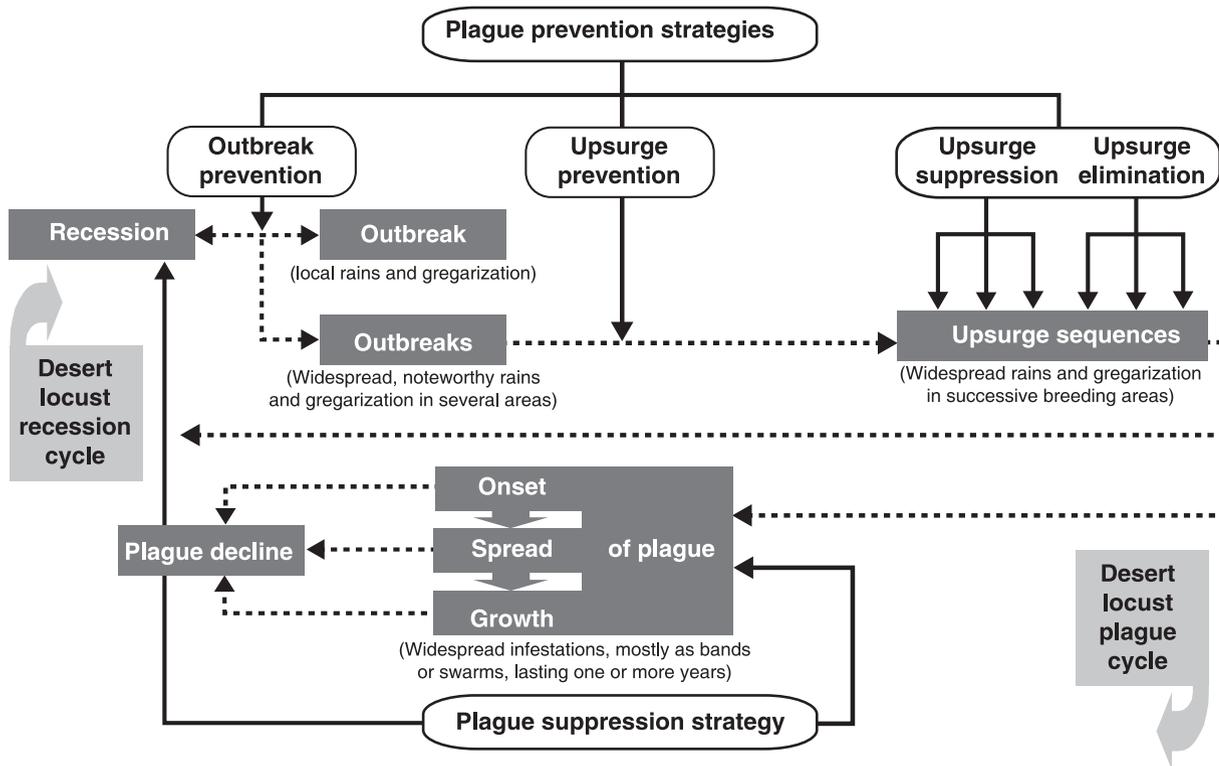
Figure 3 Desert locust control strategies (modified after Posamentier & Magor, 1997).

to post-gregarization developments. Showler termed control during a plague reactive. His claim that control between 1986 and 1989 was reactive and not initially proactive is puzzling because contemporary accounts consider that the upsurge did not become a plague until late 1987 (FAO, 1987, 1989). Ould Babah (1997) also limited the term preventive control to outbreak prevention. He used the term curative for interventions during upsurges and plagues, and palliative for control to protect cultivated zones. In contrast, Bennett (1974, 1975, 1976) provided plausible evidence from her analysis of the 1966–1969 upsurge and short plague suggesting that when rains continue to promote population growth, only upsurge elimination (Figure 3), control when all populations are gregarious, will prevent a plague. The implications of her findings are that outbreak and upsurge prevention will fail when such rains occur.

The Guidelines (FAO, 2001c: 5) encompass all the above views, stating that ideally, limited control of gregarizing populations during recessions and outbreaks should prevent upsurges. Failing this, the hope is that upsurges will be contained by ground control before they develop into a plague. The guidelines acknowledge the difficulty of controlling early upsurge populations by adding, 'In practice, it is difficult to find and treat enough of the numerous and often small and transient infestations, many of which may

consist of large numbers of scattered locusts that are poor targets.' When this occurs, major aerial campaigns are required to end the upsurge or to suppress the onset stages of a plague (FAO, 2001c: 9).

One or more years may separate the first rains that initiate high levels of multiplication from the establishment of a major plague, and the apposite time to intervene continues to be hotly debated. Three potential strategies have proponents: outbreak prevention, upsurge prevention, and upsurge elimination (Figure 3). During emergencies since 1964, while good seasonal rains continued, all three strategies were used sequentially. A fourth term, upsurge suppression, is included here to distinguish the effects of control early in an upsurge from upsurge elimination.

The case for upsurge elimination

Bennett (1975, 1976) based her advocacy of upsurge elimination on an analysis of rains that promoted successful breeding and the impact of control campaigns at different stages of plague development between 1966 and 1969. She identified four migration circuits containing gregarizing populations in 1966 that became interlinked by inter-regional migrations of adults from the autumn of 1967. Two were on the Arabian Peninsula, a third linked the western Red Sea coast with the interior of the Sudan, and

Figure 4 A sequence of breeding by desert locusts. The first generation, F_0, bred in early 1967, and the F_6 generation in late 1968. There is no evidence of breeding by F_7 adults. Arrows indicate direction of displacement between generations. Breeding areas are not drawn to scale (Bennett, 1976).
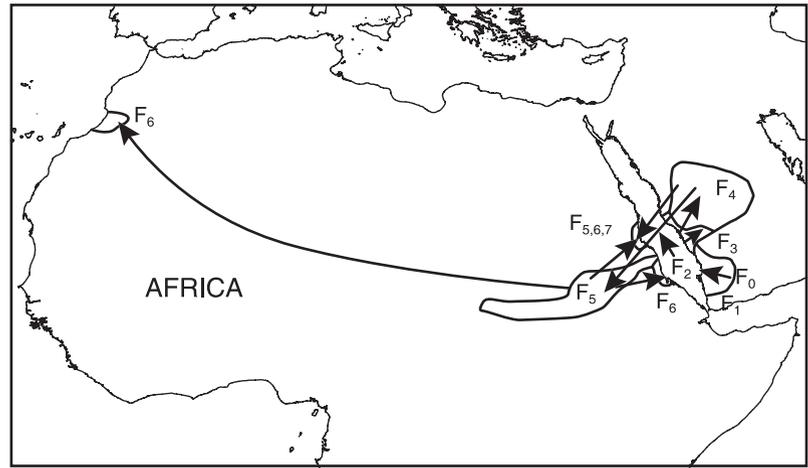
the fourth linked the mountains of Tibesti and southern Algeria with each other and with the Sahel. The main upsurge sequence was initiated by unusually heavy rains (averaging 170 mm) in south-western Arabia from March to May 1967 (Figure 4, F_0). Bennett traced this sequence for seven generations mainly in the north central region until the plague suddenly declined in late 1968 and early 1969. The F_0 and F_1 generations in south-western Arabia in the spring and summer of 1967 were largely unreported. Subsequently, Bennett found that the estimated gross infested area first expanded very rapidly from 20 000 km² along the Red Sea coasts to over a 100 000 km² in the Saudi interior, as population estimates increased from less than 1×10^9 to 6×10^9

locusts (Figure 5, F_2–F_4). Subsequently, the gross infested area shrank dramatically, as the locusts became increasingly gregarious. Bennett estimated that almost half of the F_4 population moved eastwards from Arabia. The rest remained in the main sequence and the shortfall was only partially offset by about 50 km² of swarms arriving from another sequence. The gross infested area of the bands fell through 10 000 km² to 5000 km² as numbers continued to grow from 18×10^9 (F_5) to 30×10^9 (F_6). It was at this point that aerial campaigns and large-scale barrier treatment of bands began, numbers fell, and the sequence and plague ended rapidly (Figure 5).

Bennett concluded that control against early gregarizing populations left sufficient non-target scattered locusts
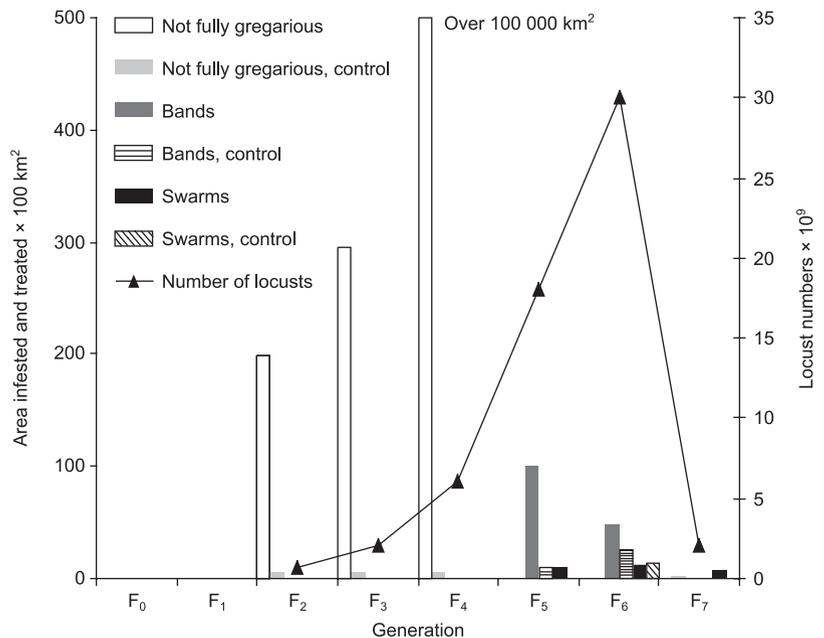
Figure 5 Areas infested by different desert locust population types and areas treated during the upsurge sequence illustrated in Figure 4 (after Bennett, 1974, 1975, 1976).

alive to continue the upsurge from autumn 1967 to mid-1968 (Figure 5, F_2–F_4), a period when rains continued to favour population increase and gregarization. She accepted that killing the gregarious and gregarizing portions of a population prevented swarm formation in Tamesna in autumn 1967, but counterclaimed that reducing the number of adults gave rise to a widespread and still predominately non-gregariously behaving progeny. Whereas, arguably an unculled progeny would have formed bands and swarms that would have been cheaper and easier to find and to control.

Bennett coined the phrase upsurge elimination for the control of fully gregarious populations infesting a greatly reduced area at the end of an upsurge and the beginning of a plague (Figure 3) and recommended withholding all control, other than crop protection until this stage. She opposed outbreak prevention on grounds of the large area (4000 km^2) that had to be blanket sprayed to kill an estimated 150 million non-gregarious hoppers in early 1969. Two infested zones were sprayed using 10 times more pesticide than needed to barrier spray the same area to kill marching bands. The locusts present were sufficient to form at most 3 km^2 of swarms, whereas the 74 000 l of dieldrin used to stop this incipient outbreak was about half that used to destroy approximately 400 km^2 of swarms in the main upsurge sequence.

Roffey (1982) could not confirm or refute Bennett's findings on plague dynamics with the data collected during the 1977–1979 plague upsurge. Inter-related financial, technical, and organizational inadequacies at national, regional, and international levels and political instability in swarm-producing areas resulted in a failure to monitor, report, forecast, and control many early populations. Consequently, the feasibility of early control was untested during this emergency. He did confirm, however, that chemical control was effective against the later fully gregarious generations and helped end the upsurge. These final campaigns were mounted with emergency assistance. Neither Bennett nor Roffey discussed the timeliness of delivering assistance and its impact on plague prevention.

The case for early intervention

Upsurge elimination, or delaying control until the population is within well-defined targets, is counterintuitive. Conversely, outbreak and upsurge prevention are psychologically appealing, as immediate action normally minimizes problems that develop and grow over time. The unanswered question for desert locust plague prevention is whether these strategies are attainable at reasonable financial and environmental costs.

Most campaign managers advocate retaining the interim strategy of controlling gregarizing populations (FAO, 1969)

and ultimately expect to achieve outbreak or upsurge prevention (Ould Babah, 1997; Showler, 1997). Others (Lecoq et al., 1997; Lecoq, 2001, 2003) advocate intervening from the outbreak stage to prevent the problem worsening and speculate that early control of the 1988–1989 plague was a major factor in its swift decline. They fear that the unculled populations associated with upsurge elimination might be too large to return rapidly to recession levels. They welcome the reintroduction of barrier treatments suggesting that their definition of preventive control extends into later stages of an upsurge when marching hopper bands will be present. They recommend giving priority to hopper band control as being easier and more certain than waiting to control swarms that migrate. Finally, they observe that preventive control has never been implemented simultaneously in the early stages of an upsurge throughout the desert locust area, a factor often due to political instability within key breeding areas.

Bennett (1976) raised three objections to waiting with the control of fully gregarious populations. First, she agreed that the larger unculled infestations might be too large for teams to destroy rapidly. Second, although the gross infested area requiring treatment decreases with gregarization, the area that must be searched to find them does not necessarily diminish. She emphasized this point because the cost of locating infestations can exceed those for subsequently spraying them. Finally, she conceded that implementing this policy could create a series of practical, but very real, political and sociological difficulties. These included the need for joint funding by beneficiaries of upsurge elimination, protests if large populations were left untreated, and the danger of crop losses during the early stages of upsurges. Damage was largely absent or at least unrecorded in her study period but might become more likely as agricultural development spreads within the recession area. We add another largely unanalysed factor, the lack of funding to mobilize sufficient and appropriately equipped control teams as an upsurge starts listed as a key requirement for ensuring sustainable preventive control (Lecoq, 2001, 2003).

Optimizing management interventions

Paradoxically, the proponents of early control and of upsurge elimination both cite decreased environmental risk and economy of cost among the advantages of their strategy. This dichotomy needs clarification and resolution so that locust control managers can adjust their responses to crop-protection protocols associated with integrated pest management where locust spraying could jeopardize the balance achieved between pests, their natural enemies, and crop tolerance to pest damage.

In contrast to many authors and to adopted policy, we consider that infrequent, large-scale upsurge campaigns are an inevitable product of the locust's environment and plague development cycle and that the early upsurge population structure prevents a swift return to economically acceptable population levels at environmentally and financially affordable costs. Lack of quantitative studies preclude a rigorous evaluation of the role early upsurge suppression campaigns played on the rapid decline of all plagues since the 1960s. In addition, discussions on plague dynamic stages and strategies are difficult while no quantitative definitions for them exist.

Experience indicates that all locusts have upsurges when habitats favour population growth for a sufficient number of generations. Plague prevention worked well for the red and migratory locusts in Africa (Roy, 2001) and the subspecies *Locusta migratoria capita* (Saussure) in Madagascar (Lecoq, 2001) from the 1960s when improved control techniques were applied in their outbreak areas. Nevertheless, campaigns of varying intensity were required to suppress outbreaks, upsurges, and incipient plagues within these permanently infested outbreak area(s). In Africa, upsurges occurred in the main *Locusta* outbreak area in Mali and elsewhere (Betts, 1961; Batten, 1966). Farrow (1987) concluded that man-made changes are responsible for higher numbers of African migratory locust infesting agricultural areas than undisturbed habitats. He also notes that upsurges or short plagues occurred in Angola in 1978–1979 and 1982–1983, in the Lake Chad Region in 1978–1979 and 1979–1980, in the Sudan in 1968–1970, 1980, and 1985, and in Southern Africa in 1970, 1980, 1983, and 1985. In Madagascar a short-lived plague occurred from 1960 to 1962 and large-scale campaigns (>100 000 ha treated annually) occurred from 1980 to 1982 and from 1987 to 1989 (Randriamanantsoa, 1997). The smaller areas treated from 1991 to 1994 were cited as an example of plague prevention by Randriamanantsoa (1997) and as an upsurge by Lecoq (2001). The plague from 1997 to 1999 was attributed to the efficiency of the control organization having declined from lack of support during a long plague-free though not upsurge-free period (World Bank, 1998; Duranton et al., 2000; Lecoq, 2001). Bahana & Byaruhanga (1999) summarized the numerous red locust upsurges between 1950 and 1988 that arose in recognized and other outbreak areas.

The fact that upsurges still occur in species that have permanent outbreak areas emphasizes the need to look again at expectations that outbreak or upsurge prevention is attainable for the desert locust under all rainfall patterns. The conclusion that sequences of above-average rains lasting for several successive generations, first initiate outbreaks and later give rise to plague upsurges (Waloff, 1966; Bennett, 1976; Roffey, 1982) suggest that destroying only the gregarizing aggregations within these initially mainly solitarious populations will not prevent upsurge developments continuing until the sequences of favourable rains in complementary breeding areas also stop. Spraying an entire infested area, as in 1969, as an alternative approach for achieving upsurge prevention was considered financially costly by Bennett (1976) and environmentally unacceptable by Ashall (1985).

Advocates of early control tacitly assume that plagues were prevented between 1960 and 1985 without accounting for the period's low rainfall and serious droughts in curtailing locust numbers. Ashall (1985), in arguing the case for upsurge elimination, contrasted the 1972–1974 upsurges that lacked widespread rains in successive complementary breeding areas with the periods 1966–1968 and 1977–1978, when rains continued until increases in the resultant upsurge populations warranted emergency plague warnings. Plague development is expected to have false starts and many fluctuations (FAO, 1968: 86) and drought-induced termination of upsurges should not be equated with successful upsurge prevention or suppression.

Ashall (1985) recommended that FAO adopt upsurge elimination because he agreed with Courshee (1965), Maccuaig (1970), and Bennett (1976) that early, partly gregarized populations would be too extensive to spray on environmental grounds if not solely for the high financial costs involved. Consultants advising FAO rejected Ashall's recommendation and FAO retained the more conservative and highly risk averse strategy that includes controlling populations that might gregarize after breeding (FAO, 1985). Their experiences showed that gregarization was rapid and upsurge prevention (Figure 3) would be required to supplement outbreak prevention (FAO, 1985). The lack of quantitative studies as upsurge prevention changes into upsurge suppression precludes a rigorous assessment of the value of early campaigns to the rapid decline at the upsurge elimination stage of the four upsurges since the 1960s that developed into early plagues. Other studies to aid this process are discussed below.

Improving population and plague dynamics

Improving population and plague dynamics requires investment in quantitative and qualitative monitoring of the age, stage, and phase structures of desert locust populations during outbreaks, upsurges, and after control operations. Data for studies must also be collected during emergencies when human resources have become geared towards control campaigns rather than research. When plagues were present in most years, regional control organizations contained multidisciplinary research teams in which entomologists, climatologists, meteorologists, and engineers worked alongside survey and control teams in

order to understand and improve operational control. They helped evaluate campaigns and developed and implemented strategies (Joyce, 1962a, 1979; Gunn, 1979). Similar teams took part in the desert locust project that followed (FAO, 1968). Subsequently, research has been commissioned after rather than during an emergency. The current practice of time-binding and focusing research on specific localities makes it particularly difficult to study events such as upsurges that are both intermittent and change location seasonally.

Bennett (1975, 1976) coined the phrase upsurge elimination for the control of fully gregarious populations that infest a greatly reduced area at the end of an upsurge and the beginning of a plague. She concluded that spraying the initial generations of gregarizing populations left sufficient non-target scattered locusts alive to continue the upsurge. In addition, she found that the same amount of pesticide was needed to eliminate an early upsurge population expected to produce about 3 km^2 of swarms as had destroyed 200 km^2 of fully gregarious swarms as the upsurge developed into a plague. To confirm or refute Bennett's findings and hypotheses requires information on the areas infested as a locust upsurge develops, the numbers of locusts in the constituent populations, and their behaviour in relation to habitats and the stage of plague development. Without such data, managers cannot determine the effectiveness of campaign tactics at different upsurge stages nor determine the type(s) of control capacity able to deliver the desired impact safely and at reasonable financial and environmental costs. Until this is done, we will remain unable to disentangle the effects that control has on breeding success and plague prevention from the effects of the environment, such as rain and migration to unfavourable habitats.

FAO (1968: 86) emphasized the importance of developing quantitative methods able to distinguish pre-outbreak and upsurge populations in different environments in order to determine when plague prevention control is necessary. This problem still exists and affects when confident early warnings can be issued that a population explosion is in progress. Routine monitoring surveys, as practised since the 1960s, estimate similar densities from locusts counted during individual transects throughout the period of population increase that precedes upsurge-initiating gregarization. It is probable that the excellent vegetation cover noted by surveyors allows individual locusts to remain unaggregated over wide areas. Conversely, Rao (1942), who developed the survey technique, treated densities derived from transect counts differently. He averaged densities within each ecological zone being studied and reported that experience enabled him to detect the significant population rises that preceded large outbreaks from local breeding of no significance. The validity of Rao's claim needs testing.

Reviewing climate variability and the desert locust threat

The fact that recent plagues ended with upsurge elimination campaigns does not justify adopting this approach without careful scrutiny. Arguably, it does indicate that control has prevented major plagues during this period (Roffey, 1982; Lecoq et al., 1997; Lecoq, 2001). Nevertheless, the drier weather after the 1960s was associated with a rapid reversal to a global circulation pattern that existed before 1890 (Lamb, 1979; Rainey et al., 1979), an earlier period that ended with a long recession (Waloff, 1976; Rainey et al., 1979; Roffey, 1982). This again indicates that the relative roles of control, drought, and migration to unsuitable habitats on the frequency, severity, and extent of plagues since 1960 need disentangling.

Bennett recommended leaving local outbreaks untreated but this advice seems unlikely to be adopted until national campaign managers and forecasters at FAO can reliably recognize rainfall and outbreak distributions that initiate transitory outbreaks from those capable of initiating upsurges. Were her hypothesis first rigorously tested, and secondly should the weather become reliably predictable some months ahead, then decisions to leave local outbreaks uncontrolled would become tenable.

Winstanley (1973a,b) provided a useful start to the impact of weather when he investigated climatic trends in the desert locust area. He showed that seasonal winter and spring rainfall totals expressed as a percentage of the long-term mean declined from the 1950s to 1960, after which the trend reversed. During the first part of the 20th century, he identified similar low seasonal values occurring around 1900, 1920, and 1930. He also found that the winter–spring rainfall pattern was negatively correlated with summer rains in the desert locust area. High summer totals were associated with strong zonal circulation in the mid-tropospheric circumpolar westerlies because this circulation pattern allowed the Inter-Tropical Convergence Zone to move farther north than normal. In contrast, a weak zonal circulation suppressed the northward extent of the ITCZ and of summer rainfall but brought rain-bearing depressions farther south during the winter and spring.

Fluctuations of varying periods were evident, and Winstanley (1973a,b) found that the highly significant statistical correlation between winter–spring and summer rainfall in individual years accounted for only about a third of the variance. His data revealed periods from 1905 to 1910, in the late 1940s, the late 1950s, and early 1960s when both rains were positively correlated. Regardless of trends, the 5-year means of both seasons' rains were at some times above and at other times below normal; these scenarios are likely to be associated with locust population numbers rising and falling, respectively. Follow-up studies have not yet been attempted.

Achieving sustainable plague prevention

The plague prevention strategy confirmed in 1985 (FAO, 1985) recommends that countries within the recession area mount plague prevention campaigns to achieve either outbreak and upsurge prevention. Should this fail, then teams are also expected to mount at least the initial upsurge suppression campaigns using national and regional reinforcements where necessary. Ashall (1985) estimated that national control managers would have about 8 months to mobilize an emergency supply of vehicles, insecticides, and application machinery from local, regional, and international sources to mount upsurge elimination campaigns. Ashall did not discuss the role national and regional reserves were expected to play before international assistance arrived. Nor did he examine the time taken from launching an appeal to operational deployment of the resulting assistance. These factors clearly affect the ability to mount large-scale campaigns in all but the richest countries and need investigating. Raising funds for earlier campaigns was not explored by Ashall (FAO, 1985; Roy, 1985).

Roffey (1982) found that during the 1977–1979 emergency, external funds to enable teams to mount large upsurge campaigns did not arrive until populations were fully gregarious. In addition, early control was hampered by security problems and too few fully equipped permanent control teams. Consequently, only upsurge elimination was fully implemented. Inadequate early control may be a recurrent feature linked to funding shortfalls and delays inherent in raising external funds to reinforce national control capacity. Bennett (1976) concluded that an aerial campaign using the barrier technique would have been successful against the F_5 hopper bands in the Sudan but did not report whether the delay in starting aerial spraying against this generation was related in any way to the arrival of external assistance. A study on the effect of raising reserve and emergency funding on delaying appropriate early upsurge campaigns is long overdue.

Campaign evaluations to assess the impact of control, drought, and migration to unsuitable habitats on ending upsurges need to become an integral part of campaign management as they were during plague suppression campaigns. Data for investigating plague development and testing management practices can be collected only during upsurges. Consequently, data collecting and analysis of campaigns need to become routine procedures before the next upsurge which, as experience shows, is likely to occur with little warning.

Desert locust control has, to date, required external funding to re-equip teams and to finance large-scale campaigns (Uvarov, 1951; Lean, 1965; FAO, 1970, 2004b). This underlying financial shortcoming causes delays between appeals being launched, money being pledged and resources being delivered. Interest in and funds for research increase during plagues and fall during recessions. As a result, anti-locust technology changes during and shortly after each plague but funds to equip and train locust teams to use it do not arrive until the next upsurge is well underway. Consequently, control teams are ill equipped and ill prepared to use the latest techniques each time a plague upsurge begins, and the emergency in 2003–2005 was no exception (FAO, 2004b).

An increased awareness that chemical pesticides may cause environmental pollution arose during the 1985–1989 plague and funds became available to develop biopesticides, to improve spraying techniques (see above, 'Control methods'), to invest in ecotoxicological research and monitoring systems, as well as to use computers to manage locust, weather, and habitat data used in the early warning system. None of these improvements was fully operational in 2003 when the next emergency started.

The basic early warning system, collecting, transmitting, and analysing information on locusts, weather, and habitat remains unchanged but these data are now displayed in computer based geographical information systems (GIS). Field observations recorded in hand-held computers can now be transmitted into the national GIS for display in conjunction with observed and estimated environmental conditions. Satellite imagery products are routinely transmitted between computers in FAO and in affected countries. The reliability with which the improved processing identifies vegetation remains largely untested. Extensive ground truthing exercises are essential if locust units are to confidently relate imagery signatures to vegetation able to provide locust breeding habitats. Incorporation and analysis of the spray data generated during the recent emergency by GPS linked control technology has yet to be incorporated in current operational systems.

The operational GIS routines and import/export programmes are designed to facilitate interchange of an agreed set of data. Consequently, changes must be planned carefully to avoid potentially costly changes to database structure, to GIS routines, and to maintain seamless interchange between the national systems and the one at FAO. These customized systems also require ongoing support and maintenance. To date, FAO has found cover for annual commercial maintenance contracts and for developers to continue to meet system requirements. This has enabled the GIS developers to implement functionality that meets the changing needs and aspirations of users.

Computer management of data is now an established feature of the desert locust early warning system. There is less evidence of the systems being used in a more generic way to generate analyses of the impact of control campaigns and peer reviewed case studies of locust events. Such

research requires greater knowledge of GIS than users need for routine operational use. The 2003–2005 upsurge revealed that countries invaded solely during upsurges and plagues lacked training in data collection, analysis, and transmission and would benefit from a GIS to manage their data and forward it to FAO in a suitable format. These are issues to be considered and resolved before the next upsurge.

The desert locust component of the FAO EMPRES for transboundary animal and plant pests and diseases was initiated in 1995 to strengthen the capacity of the national, regional, and international components of the desert locust management and early warning systems to implement effective and efficient preventive control strategies using timely and environmentally sound interventions. Whichever tactic is employed, preventive control requires a national survey and control capacity maintained in operational readiness and procedures able to mobilize national, regional, and international reinforcements rapidly. In addition, improved technologies have to be tested, adopted, and incorporated into working practices. This degree of preparedness has proven elusive in the past; EMPRES offers a further opportunity to achieve sustained improvements.

References

Allan W (1931) Locust in northern Rhodesia. Annual Bulletin Department Agriculture Northern Rhodesia 1: 6–11.

Ashall (1985) The resources needed for Desert Locust plague prevention in the Central Region of its distribution area. Unnumbered AGP Consultant's Report. FAO, Rome, Italy.

Bahana JW & Byaruhanga EK (1999) Advances and review strategies for Red Locust plague prevention: the control of Red Locust *Nomadacris septemfasciata* (Serville) into the 21st Century. Insect Science and its Application 19: 265–272.

Batten A (1966) The course of the last major plague of the African Migratory Locust 1928 to 1941. FAO Plant Protection Bulletin 14 (1): 1–16.

Bennett LV (1974) Factors Affecting the Upsurge and Decline of Populations of the Desert Locust (*Schistocerca gregaria* Forskål) in 1966–1969. PhD Thesis, University of London, London, UK.

Bennett LV (1975) Development of a desert locust plague. Nature 256: 486–487.

Bennett LV (1976) The development and termination of the 1968 plague of the Desert Locust. Bulletin of Entomological Research 66: 511–552.

Besnault C (1962) Rapport sur les activité de Groupe aérien de Lutte antiacridienne No. 2 au Sénégal et en Mauritanie en septembre et octobre 1960. International Agricultural Aviation Congress, Grignon (1962) 2: 219–227.

Betts E (1961) Outbreaks of the African Migratory Locust (*Locusta migratoria migratorioides* R & F) since 1871. Anti-Locust Memoir No. 6. Anti-Locust Research Centre, London, UK.

Bhatia GN (1961) Observations on concentrated solitary breeding of Desert Locust (*Schistocerca gregaria* Forsk.) in Rajasthan (India) during 1956. Indian Journal of Entomology 21: 77–81.

Brussels (1938) Comptes rendus de la 5me conférence internationale pour les recherches antiacridiennes, Bruxelles, 1938. Ministère des Colonies, Brussels, Belgium.

Cairo (1937) Recommendations adopted by the conference no. 3. Plan for the permanent supervision of the outbreak areas of the Desert Locust, *Schistocerca gregaria* (Forskål). Proceedings of the 4th International Locust Conference, Cairo, 1936, pp. 83–84. Government Press, Bulâq, Cairo, Egypt.

Cochemé J (1966) Wind opportunities for locust transport and concentration in India and West Pakistan, June 20–30, 1961. A Case Study of an Invasion of the Summer Breeding Area of the Desert Locust. Progress Report No. UNSF/DL/RFS/6. FAO, Rome, Italy.

Courshee RJ (1965) Chemical Control – technical studies. Final report of the operational research team of the United Nations Special Fund Desert Locust Project. Vol. 1, pp. 206–285. FAO Progress Report No. UNSF/DL/OP/5. FAO, Rome, Italy.

Courshee RJ (1990) Desert Locust and their control. International Pest Control 32: 16–18.

Desert Locust Survey (1956) Report of the Desert Locust Survey, 1 June 1953–30 June 1955. East Africa High Commission, Nairobi, Kenya.

Despland E & Simpson SJ (2000) The role of food distribution and nutritional quality in behavioural phase change in the desert locust. Animal Behaviour 59: 643–652.

Duranton J-F, Razafindratsima A, Franc A & Lecoq M (2000) Spread of a migratory locust plague in Madagascar. Proceedings of the XXI International Congress of Entomology, Foz do Iguaçu, Brazil, August 20–26, 2000. Abstract Book 1 (ed. by DL Gazzoni). Embrapa, Londrina, Brazil.

Elliott CCH (2000) FAO's perspective on migratory pests. Workshop on Research Priorities for Migrant Pests of Agriculture in Southern Africa, Plant Protection Research Institute, Pretoria, South Africa, 24–26 March 1999 (ed. by RA Cheke, LJ Rosenberg & ME Kieser), pp. 17–24. Natural Resources Institute, Chatham, UK.

FAO (1956) FAO Panel of Experts on the long-term policy of Desert Locust control, London, April 1956. Report No. 1956/11. FAO, Rome, Italy.

FAO (1959) FAO Panel of Experts on the strategy of Desert Locust plague control, Rome, April–May 1959. Report No. 1959/5. FAO, Rome, Italy.

FAO (1967) The Current Desert Locust Recession and FAO's Policy of Control and Prevention, by Gurdas Singh. Report No. PL/DL/1-Rev.1. FAO, Rome, Italy.

FAO (1968) Desert Locust Project Final Report. Report No. FAO/SF:34/DLC. FAO, Rome, Italy.

FAO (1969) Thirteenth Session of the Desert Locust Control Committee, Rome, 1969. Report No. PL/1969/M/5. FAO, Rome, Italy.

FAO (1970) FAO's role in international coordination of locust research and control by Gurdas Singh. Report No. AGP/DL/1. FAO, Rome, Italy.

FAO (1980) Trilingual glossary of terms used in acridology. No.

AGP/DL/TS/21. Plant Production and Protection Division, Locust Control – Desert Locust Programme. FAO, Rome, Italy.

FAO (1985) Consultation on Desert Locust plague prevention in the Central Region, Rome, May, 1985. Report unnumbered. FAO, Rome, Italy.

FAO (1987) The Desert Locust [in 1986]. Migrant Pest Newsletter 51–52: 1–7.

FAO (1989) The Desert Locust [in 1987]. Migrant Pest Newsletter 53–54: 1–4.

FAO (1996) Evaluation of field trials data on the efficacy and selectivity of insecticides on locusts and grasshoppers. Report to FAO by the Pesticide Referee Group. Fifth meeting, 20–22 September 1995. FAO, Rome, Italy.

FAO (1997) Evaluation of field trials data on the efficacy and selectivity of insecticides on locusts and grasshoppers. Report to FAO by the Pesticide Referee Group. Sixth meeting, 10–12 December 1996. FAO, Rome, Italy.

FAO (1998) Economic and policy issues in Desert Locust management: a preliminary Analysis by S Joffe. FAO Report No. AGP/DL/TS/27, pp. 15–131. FAO, Rome, Italy.

FAO (2001a) Biology and behaviour by PM Symmons & K Cressman. Desert Locust Guidelines, Vol. 1. FAO, Rome, Italy. Also at URL://www.fao.org/ag/locusts/en/info/info/index.html then use publications link.

FAO (2001b) Control by HM Dobson. Desert Locust Guidelines, Vol. 4. FAO, Rome, Italy. Also at URL://www.fao.org/ag/locusts/en/info/info/index.html then use publications link.

FAO (2001c) Campaign organization and execution by PM Symmons & K Cressman. Desert Locust Guidelines, Vol. 5. FAO, Rome, Italy. Also at URL://www.fao.org/ag/locusts/en/info/info//index.html then use publications link.

FAO (2001d) Appendices by K Cressman & HM Dobson. Desert Locust Guidelines, Vol. 7. FAO, Rome, Italy. Also at URL://www.fao.org/ag/locusts/en/info/info/index.html then use publications link.

FAO (2003) Desert Locust population dynamics parameters. Report No. AGP/DL/TS/30. FAO, Rome, Italy. Also at URL://www.fao.org/ag/locusts/en/info/info/index.html then use publications link.

FAO (2004a) Evaluation of field trials data on the efficacy and selectivity of insecticides on locusts and grasshoppers. Report to FAO by the Pesticide Referee Group. Ninth meeting, 18–21 October 2004. FAO, Rome, Italy. Also at URL://www.fao.org/ag/locusts/en/info/info/index.html then use publications link.

FAO (2004b) Extraordinary Session of the FAO Desert Locust Control Committee, Rome, 2004. FAO, Rome, Italy.

Farrow RA (1987) Effects of changing land use on outbreaks of Tropical Migratory Locust, *Locusta migratoria migratorioides* (R & F). Insect Science and its Application 4: 6: 969–975.

Faure JC (1923) The life-history of the Brown Locust, *Locusta pardalina* (Walker). Journal of the Department of Agriculture Union of South Africa 7: 205–224.

Gilot J (1965) Utilisation des aéronefs dans la lutte antiacridienne au Maroc. Comptes Rendus des Travaux du Congrès sur la Protection des Cultures Tropicales, pp. 273–276.

Guichard KM (1955) Habitats of the Desert Locust (*Schistocerca gregaria* Forskål) in western Libya and Tibesti. Anti-Locust Bulletin 21, 32 pp.

Gunn DL (1979) Setting the scene: the development of aircraft attack on locust swarms in Africa since 1945 and the start of operational research on control systems. Strategy and Tactics of Control of Migrant Pests: A Royal Society Discussion held on 29 and 30 June 1977, London (ed. by DL Gunn & RC Rainey), pp. 3–15. Royal Society, London, UK.

Harris WV (1933) The Red Locust. Pamphlet Department of Agriculture Tanzania 10.

Hemming CF, Popov GB, Roffey J & Waloff Z (1979) Characteristics of Desert Locust plague upsurges and discussion on alternative hypotheses. Strategy and Tactics of Control of Migrant Pests: A Royal Society Discussion held on 29 and 30 June 1977, London (ed. by DL Gunn & RC Rainey) pp. 127–138, 167–179. Royal Society, London, UK.

van Huis A (1994) (ed.) Desert locust control with existing techniques: an evaluation of strategies. Proceedings of the Seminar held in Wageningen, The Netherlands, 6–11 December 1993. Wageningen University, Wageningen, The Netherlands.

Hussein M (1938) An expedition to Arabia for locust investigations. Comptes rendus de la 5eme conférence internationale pour les recherches antiacridiennes, pp. 345–566. Ministère des Colonies, Brussels, Belgium.

Jackson GT, Popov GB, Ibrahim AO, Alghamedi SA & Khan AM (1978) Effect of natural food plants on the development, maturation, fecundity and phase of the desert locust, *Schistocerca gregaria* (Forskål). Miscellaneous Report, No. 42. Centre for Overseas Pest Research, London, UK.

Janssen JAM (1993) African Armyworm Outbreaks: Why Do They Occur after Droughts? PhD thesis, Wageningen Agricultural University, Wageningen, The Netherlands.

Joffe SR (1995) Desert Locust management, a time for change. World Bank Discussion Paper No. 284. World Bank, Washington DC, USA.

Johnston HB (1926a) New facts regarding the phases of migratory locusts. Nature 118: 10–11.

Johnston HB (1926b) A further contribution to our knowledge of the bionomics and control of the Migratory locust *Schistocerca gregaria* Forsk. (*peregrina* Oliv.) in the Sudan. Bulletin Welcome Tropical Research Laboratories (Entomology) No. 22.

Joyce RJV (1962a) Control operations. Report of the Desert Locust Survey 1 June 1955–31 May 1961, pp. 11–45. East Africa Common Services Organization, Nairobi, Kenya.

Joyce RJV (1962b) The sizes of locust populations. Chapter 5. Research Report of the Desert Locust Survey, 1 June 1955–31 May 1961, pp. 48–61. East African Common Services Organization, Nairobi, Kenya.

Joyce RJV (1979) The evolution of an aerial application system for the control of Desert Locusts. Strategy and Tactics of Control of Migrant Pests: a Royal Society Discussion held on 29 and 30 June 1977, London (ed. by DL Gunn & RC Rainey) pp. 57–66. Royal Society, London, UK.

Karrarr AMHM (1974) Study of the 1972/73 upsurge of the Desert Locust (*Schistocerca gregaria* (Forsk.)) and the effect of the control operations undertaken by national and international Organizations. Eighteenth session of the FAO Desert

Locust Control Committee, Rome, 1974. Working Paper No. AGP: LCC/74/3. FAO, Rome, Italy.

Kennedy JS (1939) The behaviour of the Desert Locust (*Schistocerca gregaria* (Forsk.)) (Orthopt.) in an outbreak centre. Transactions of the Royal Entomological Society, London 89: 385–542.

Krall S, Peveling R & Ba Diallo D (1997) (eds.) New Strategies in Locust Control. Birkhauser-Verlag, Basel, Switzerland.

Lamb HH (1979) Discussion. Strategy and Tactics of Control of Migrant Pests: A Royal Society Discussion held on 29 and 30 June 1977, London (ed. by L Gunn & RC Rainey), pp. 92–94. Royal Society, London, UK.

Lean OB (1931) On the recent swarming of *Locusta migratorioides* R. & F. Bulletin of Entomological Research 22: 365–378.

Lean OB (1936) *Locusta migratoria migratorioides* R. & F.: an ecological reconnaissance of the suspected Middle Niger outbreak area. Bulletin of Entomological Research 27: 105–184.

Lean OB (1965) FAO's contribution to the evolution of international control of the Desert Locust 1951–1963. Desert Locust Newsletter, Special Issue 1965. FAO, Rome, Italy.

Lecoq M (2001) Recent progress in Desert in Migratory Locust management in Africa. Are preventive actions possible? Journal of Orthoptera Research 10: 277–291.

Lecoq M (2003) Desert Locust threat to agricultural development and food security and FAO's international role in its control. Arab Journal of Plant Protection 21: 188–193.

Lecoq M, Duranton J-F & Rachadi T (1997) Towards an integrated strategy for the control of the desert locust. New Strategies in Locust Control (ed. by S Krall, R Peveling & D Ba Diallo), pp. 467–473. Birkhäuser Verlag, Basel, Switzerland.

London (1934) Proceedings of the 3rd International Locust Conference, London, September 1934. Cmd. 4725. His Majesty's Stationery Office, London, UK.

MacCuaig RD (1970) Locust control – the economic impact of new technologies. The technological economics of crop protection and pest control. Monograph No. 36, pp. 119–128. Society of Chemical Industry, London, UK.

Mallamaire A & Roy J (1959) La lutte contre le criquet pèlerin (*Schistocerca gregaria* Forsk.) en Afrique occidentale française. Bulletin de la Protection des Végétaux, Dakar (1958) 5: 1–113.

Malual AG, Hassanali A, Torto B, Assad YOH & Njagi PGN (2001) The nature of the gregarizing signal responsible for material transfer of phase to the offspring in the desert locust. Journal of Chemical Ecology 27: 1423–1435.

Maxwell-Darling RC (1936) The outbreak centres of *Schistocerca gregaria* Forsk. on the Red Sea Coast of the Sudan. Bulletin of Entomological Research 27: 37–66.

Maxwell-Darling RC (1937) The outbreak areas of the Desert Locust (*Schistocerca gregaria* Forsk.) in Arabia. Bulletin of Entomological Research 28: 605–618.

McCaffery AR, Simpson SJ, Islam M & Roessingh P (1998) A gregarizing factor present in the egg pod foam of the desert locust *Schistocerca gregaria*. The Journal of Experimental Biology 201: 347–363.

Ould Babah MA (1997) Strategy for controlling the Desert Locust in Mauritania. New Strategies in Locust Control (ed. by S Krall, R Peveling & D Ba Diallo), pp. 487–491. Birkhäuser-Verlag, Basel, Switzerland.

Paris (1932) Procès-verbal des séances de la 2eme conférence internationale pour les recherches anti-acridiennes. Editions de la Société Entomologique de France, Paris, France.

Pedgley DE & Symmonds PM (1968) Weather and the locust upsurge. Weather 23: 484–493.

Perrot J (1956) Remarques sur quelques nouveaux moyens de lutte contre les sauterelles adultes. Terre Marocaine 30: 248–251.

Popov GB (1968) Locust survey in Oman, 11 January to 3 March, 1968. Occasional Report. No. 13/68. Anti-Locust Research Centre, London, UK.

Popov GB, Jackson G, Ibrahim A, Alghamedi S & Khan A (1978) Effect of the food plant on gregarization in the desert locust (*Schistocerca gregaria* (Forskål)). COPR Miscellaneous Report No. 40. Centre of Overseas Pest Research, London, UK.

Posamentier H & Magor J (1997) Results and recommendations of the working group Management Strategies. New Strategies in Locust Control (ed. by S Krall, R Peveling & D Ba Diallo), pp. 515–517. Birkhäuser-Verlag, Basel, Switzerland.

Rainey RC (1951) Weather and the movement of locust swarms: a new hypothesis. Nature 168: 1057–1060.

Rainey RC (1963) Meteorology and the migration of Desert Locusts. Applications of synoptic meteorology in locust control. Anti-Locust Memoir No. 7. Anti-Locust Research Centre, London, UK, and WMO Technical Note. No. 54. World Meteorological Organization, Geneva, Switzerland.

Rainey RC (1965) Seasonal and longer-period changes in the Desert Locust situation (with a note on a tropical cyclone affecting southern Arabia in 1948). Meteorology and the Desert Locust. WMO Technical Note No. 69: 255–264. World Meteorological Organization, Geneva, Switzerland.

Rainey RC & Betts E (1979) Problems of alternative hypotheses and discussion on alternative hypotheses. Strategy and Tactics of Control of Migrant Pests: a Royal Society Discussion held on 29 and 30 June 1977, London (ed. by DL Gunn & RC Rainey), pp. 111–126, 167–179. Royal Society, London, UK.

Rainey RC, Betts E & Lumley A (1979) The decline of the Desert Locust plague in the 1960s: control operations or natural causes? Strategy and Tactics of Control of Migrant Pests: A Royal Society Discussion held on 29 and 30 June 1977, London (ed. by DL Gunn & RC Rainey), pp. 67–91. Royal Society, London.

Randriamanantsoa M (1997) Histoire de la lutte antiacridienne à Madagascar (ed. by R Scherer & L Fong Hong), pp. 49–71. Symposium sur la lutte antiacridienne à Madagascar., Antananarivo, Madagascar, Projet DPV-GTZ 'Promotion de la Protection Intégrée des Cultures et des Denrées Stockées'. TSIPIKA Editeur, Antananarivo, Madagascar.

Rao YR (1937a) The studies of migration among solitaries of the Desert Locust (*Schistocerca gregaria* Forsk.). Appendix 10, ILC No. 15. Proceedings 4th International Locust Conference, Cairo, 1936. Government Press, Bulâq, Cairo, Egypt.

Rao YR (1937b) Some outbreak centres of *Schistocerca* in Mekran. Appendix 30, ILC No. 1. Proceedings 4th International Locust Conference, Cairo, 1936. Government Press, Bulâq, Cairo, Egypt.

Rao YR (1942) Some results of studies on the Desert Locust (*Schistocerca gregaria* Forsk.) in India. Bulletin of Entomological Research 33: 241–265.

Rao YR (1960) The Desert Locust in India. Indian Council of Agricultural Research, New Delhi, India.

Rodgers SM, Matheson T, Anstey M & Simpson SJ (2005) Early induction of behavioural phase change in the Desert Locust. Abstracts of the Ninth International Conference of the Orthopterists' Society. Metaleptea (special Meeting Issue): 71. Canmore, Canada.

Roffey J (1965) Nature and scale of the desert locust problem and survey costs. Operational Research. Final Report – Vol. 1: pp. 173–205. United Nations Special Desert Locust Project Progress Report. No. UNSF/DL/OP/5. FAO, Rome, Italy.

Roffey J (1981) Outbreaks. Desert Locust Forecasting Manual, Vol. 1 (ed. by DE Pedgley), pp. 21–31. Centre for Overseas Pest Research, London, UK.

Roffey J (1982) The Desert Locust upsurge and its termination 1977–79. Desert Locust Field Research Stations, Technical Series, No. AGP/DL/TS/23. FAO, Rome, Italy.

Roffey J & Popov GB (1968) Environmental and behavioural processes in a desert locust outbreak. Nature 219: 446–450.

Roffey J, Popov G & Hemming CF (1970) Outbreak and recession populations of the Desert Locust *Schistocerca gregaria* (Forsk.). Bulletin of Entomological Research 59: 675–680.

Roffey J & Stower WJ (1983) Numerical changes in the Desert Locust, *Schistocerca gregaria* (Forskål), in a seasonal breeding area on the coasts of Eritrea. Ethiopia, with special reference to ecology and behaviour. Report No. AGP/DL/TS/24. FAO, Rome, Italy.

Rome (1931) Rapport de la réunion internationale convoquée par le Ministère des Colonies d'Italie pour l'étude du problème des acridiens migrateur, Rome, 1931. Instituto Poligraphico dello Stato, Rome, Italy.

Rosenberg LJ (1999) Regional control of the Red Locust, *Nomadacris septemfasciata* (Serville), in the first half of the 20th century. Insect Science and its Application 19: 283–289.

Roy JLH (1985) Elements of the preventive control strategy against the Desert Locust in the Central Region. Unnumbered AGP Consultant's Report. FAO, Rome, Italy.

Roy J (2001) Histoire d'un siècle de lutte anti-acridienne en Afrique: contributions de la France. l'Harmattan, Paris, France.

Sayer HJ & McCuaig RD (1961) An exchange visit to Morocco, November 1960. United Nations Special Fund Desert Locust Project. Progress Report No. UNSF/DL/V/1. FAO, Rome, Italy.

Schulten GGM (1990) Needs and constraints of integrated pest management in developing countries. Mededelingen Faculteit der Landbouwwetenschappen Rijksuniversiteit Gent 55: 207–216.

Showler AT (1997) Proaction: strategic framework for today's reality. New Strategies in Locust Control (ed. by S Krall, R Peveling & D Ba Diallo), pp. 461–465. Birkhäuser-Verlag, Basel, Switzerland.

Simpson SJ, Despland E, Hägele BF & Dodgson T (2001) Gregarious behaviour in desert locusts is evoked by touching their back legs. Proceedings of the National Academy of Science 98: 3895–3897.

Simpson SJ, McCaffery AR & Hägele B (1999) A behavioural analysis of phase change in the desert locust. Biological Review 74: 461–480.

Skaf R (1978) Etude sur les cas de grégarisation du criquet pèlerin en 1974 dans le sud-ouest Mauritanien et au Tamesna malien. Stations de Recherche acridienne sur le Terrain, Series techniques. No. AGP/DL/TS/17. FAO, Rome, Italy.

Stower WJ (1962) The phases of Locusts. Lectures of the second Desert Locust training course, Ethiopia, 1962. Report No. FAO/UNSF/DL/TC/4, pp. 6–12. FAO, Rome, Italy.

Stower WJ, Davies DE & Jones IB (1960) Morphometric studies of the Desert Locust *Schistocerca gregaria* (Forsk.). Journal of Animal Ecology 29: 309–339.

Stower WJ & Greathead DJ (1969) Numerical changes in a population of the Desert Locust, with special reference to factors responsible for mortality. Journal of Applied Ecology 6: 203–235.

Symmons PM (1992) Strategies to combat the Desert Locust. Crop Protection 11: 206–212.

Symmons PM (2003) A. Resources, spreadsheets to determine resources for outbreak, upsurge and plague campaigns. B. Simdeposit, idealised deposits from incremental ultra low volume (ULV) spraying. C. Simpatch, finding and treating hopper patches simulating outbreaks on foot and in vehicles. D. Simbandblock finding and marking hopper band block targets. FAO, Rome, Italy. http://www.fao.org/ag/locusts/en/publicat/gl/contplans/index.html

Symmons PM (2004) A computer simulation of Desert Locust band target block detection and demarcation. Crop Protection 23: 183–190.

UK delegation (1937a) The origin of the present outbreak of the African Migratory Locust, *Locusta migratoria migratorioides* (Reiche and Fairmaire) in Africa and the prevention of outbreaks. Appendix 21, ILC(UK) No. 2. Proceedings of the 4th International Locust Conference, Cairo, 1936. Government Press, Bulâq, Cairo, Egypt.

UK delegation (1937b) Further investigations on the Desert Locust *Schistocerca gregaria* (Forskal). Appendix 29, ILC(UK) No. 3. Proceedings of the 4th International Locust Conference, Cairo, 1936. Government Press, Bulâq, Cairo, Egypt.

UK delegation (1938) Scheme of the permanent international organisation for the preventive control of the Desert Locust *Schistocerca gregaria* Forsk. in Eastern Africa and Western Asia. Comptes rendus de la 5eme conférence internationale pour les recherches antiacridiennes, 1938, pp. 342–344. Ministère des Colonies, Bruxelles, Belgique.

Uvarov BP (1921) A revision of the genus *Locusta*, L (=*Pachytylus* Fieb.) with a new theory as to the periodicity and migrations of locusts. Bulletin of Entomological Research 12: 135–163.

Uvarov BP (1923) A revision of the Old World Cyrtacanthacrinae (Orthoptera, Acrididae) I, II & III. Annals and Magazine of Natural History 13: 1–19, 14: 96–113.

Uvarov BP (1933a) The locust outbreak in Africa and western Asia, 1925–1931. Publication No. 63-80-1. His Majesty's Stationery Office, London, UK.

Uvarov BP (1933b) The locust outbreak in Africa and western Asia in 1932. Publication No. 63-80-2. His Majesty's Stationery Office, London, UK.

Uvarov BP (1934) The locust outbreak in Africa and western Asia in 1933. Publication No. 63-80-3. His Majesty's Stationery Office, London, UK.

Uvarov BP (1935) The locust outbreak in Africa and western Asia in 1934. Publication No. 63-80-4. His Majesty's Stationery Office, London, UK.

Uvarov BP (1937) Biological and ecological basis of locust phases and their practical application. Proceedings 4th International Locust Conference, Cairo, 1936, Appendix 7. Government Press, Bulâq, Cairo, Egypt.

Uvarov BP (1951) Locust research and control 1929–1950. Colonial Research Publication No. 10. His Majesty's Stationery Office, London, UK.

Uvarov BP & Milnthorpe W (1937a) The locust outbreak in Africa and western Asia in 1935. Publication No. 63-80-5. His Majesty's Stationery Office, London, UK.

Uvarov BP & Milnthorpe W (1937b) The locust outbreak in Africa and western Asia in 1936. Publication No. 63-80-6. His Majesty's Stationery office, London, UK.

Uvarov BP & Milnthorpe W (1939) The locust outbreak in Africa and western Asia in 1937. Publication No. 63-80-7. His Majesty's Stationery Office, London, UK.

Varma BK & Sharma TR (1966) Effect of cyclone on locusts. Indian Journal of Entomology 28: 14–32.

Venkatesh MV (1971) A case study of the influence of a cyclone on the incursion of Desert Locusts into Rajasthan during June 1964. Indian Journal of Entomology 33: 1–16.

Volkhonsky MA & Volkhonsky MT (1939) Rapport préliminaire sur une mission d'étude des acridiens dans le Mouydir et le Tademaït (mai-juillet 1939). Archives de l'Institut Pasteur d'Algérie 17: 634–649.

Waloff Z (1966) The upsurges and recessions of the Desert Locust plague: an historical survey. Anti-Locust Memoir No. 8. Anti-Locust Research Centre, London, UK.

Waloff Z (1976) Some temporal characteristics of Desert Locust plagues. Anti-Locust Memoir No. 13. Anti-Locust Research Centre, London, UK.

Winstanley D (1973a) Recent rainfall trends in Africa, the Middle East and India. Nature 243: 464–465.

Winstanley D (1973b) Rainfall patterns and general atmospheric circulation. Nature 245: 190–194.

Woldewahid G (2003) Habitats and spatial patterns of solitarious Desert Locusts (*Schistocerca gregaria* Forsk.) on the coastal plain of Sudan. PhD Thesis. Wageningen University, Wageningen, The Netherlands. Also published in 2004 as: Tropical Resources Management Papers No. 48.

World Bank (1998) Report on the Meeting of the World Bank Panel to evaluate the Migratory Locust situation in Madagascar, 18–22 May, 1998. World Bank, Washington DC, USA.

Zolotarevsky BN (1934) Rapport préliminaire sur l'action de la mission d'études de la biologie des acridiens en 1932–34. Proceedings of the third International Locust Conference, London, 1934, Cmd. 4725, pp. 169–179. His Majesty's Stationery Office, London, UK.

Zolotarevsky BN (1938) Les subdivisions des aires grégariènes et leur rôle dans la transformation des phases (essai de classification). Comptes rendus de la 5me conférence internationale pour les recherches antiacridiennes, Bruxelles, 1938, pp. 258–264. Ministère des Colonies, Bruxelles, Belgique.