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Characteristics of Desert Locust plague upsurges

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Between plagues, the Desert Locust typically exists in low-density populations which migrate between successive breeding areas in its extensive and arid recession area. Local outbreaks develop when conditions favour concentration, multiplication and gregarization. Plagues are initiated when such conditions extend over larger areas and last long enough to allow several generations of successful breeding. Plague prevention consequently requires adequate monitoring and control of populations in the breeding areas.

1. Introduction

The outstanding biological characteristic of locusts is their ability to respond to changes in population density behaviourally, physiologically and morphologically. Individuals occurring in low-density populations typically behave like grasshoppers and belong to the solitarious phase, though seldom in the extreme form as defined by Uvarov (1966). When crowded together they undergo a transformation to the gregarious phase and form persistent assemblages of nymphs (hopper bands) or adults (swarms). The opposite of this process of gregarization is dissociation. Intermediate forms belong to the transient phase.

The theory of phase polymorphism was first advanced by Uvarov (1921) for *Locusta migratoria* (L.) and has since been shown to apply to other species. He showed that in Russia *L. migratoria* plagues started in certain restricted habitats in which locusts intermittently increased in numbers, gregarized and formed emigrant swarms. Such permanent outbreak areas were later found for two major African locusts, *Locusta migratoria migratorioides* (R. & F.) and *Nomadacris septemfasciata* (Serv.), and since the 1940s successful prevention of their plagues has been based on the surveillance of these areas.

Some points of terminology must now be explained. By a *plague* we mean a period when many countries are infested by successive generations of gregarious locusts. Plagues alternate with *recessions* when there are limited or no gregarious populations. Recessions are punctuated by *outbreaks*, or local increases in population density accompanied by gregarization which may result in the production of hopper bands and swarms; outbreaks may lead to *plague upsurges* when populations increase and gregarize on a larger scale and over several generations (Waloff 1966).

The problem of preventing plagues of the Desert Locust, *Schistocerca gregaria* (Forsk.), proved to be complex and its plagues have continued into the 1960s, with the last upsurge occurring in 1967–8. The main difficulties arise from: (1) the great mobility of Desert Locust adults in all phases; (2) the very unstable environment in the recession area; (3) the resultant continual fluctuation in numbers in, and density and phase of, recession populations; (4) the large size of the recession area and the emptiness and geographical remoteness of much of the terrain in which outbreaks and plague upsurges occur.

2. Differences between phases

The more important differences between phases have now to be considered, since the choice of strategy of plague prevention must depend on the biological attributes of populations involved in plague upsurges.

The outstanding differences between phases are *behavioural*. Gregarious hoppers form cohesive marching bands; solitarious hoppers move little, and avoid one another until they become habituated to their fellows (Ellis 1959). Gregarious adults form cohesive swarms which characteristically fly by day, maintain their separate identity for weeks (Rainey 1963) and probably often throughout their life, and extend the distribution area of the species during plagues. Solitarious and transient adults fly mainly by night, when lower temperatures restrict their distribution.

Solitarious females lay more egg pods containing more eggs than gregarious ones (Ashall & Ellis 1962, Papillon 1960). Potential multiplication rates are thus higher in solitarious populations.

Finally, crowding affects the coloration of hoppers and adults, as well as adult morphometrics, which are also affected by some environmental factors. If mature solitarious males become crowded on maturation they acquire the yellow coloration of mature gregarious locusts (Volkonsky 1938).

Changes in behaviour may be rapid but changes in colour and morphology occur more slowly. Because of fluctuating conditions in the recession area, the phase status of locust populations changes frequently and most recession populations are in the transient phase (Uvarov 1966).

3. Recession populations and outbreaks

During recessions most reports refer to hoppers and adults at low densities with occasional reports of what are described as bands and swarms. Recession populations migrate within the recession area, moving with the wind (Rao 1942) between areas of seasonal or erratic rainfall, in which they breed, and where outbreaks sometimes occur (Waloff 1966). As was recognized long ago (FAO 1956) the occurrence of these breeding and outbreak areas depends on weather systems which transport locusts and bring rain and which change from season to season. However, the incidence of outbreak conditions has been repeatedly associated with areas of marked relief in desert regions, or with areas where flying locusts may be concentrated by mobile mesoscale or larger semi-permanent convergence systems (Waloff 1972). The detailed distribution of the outbreak *sites* is determined by patterns of soil moisture and of vegetation, which promote further concentration of locusts (Popov 1965). How Desert Locust outbreaks may develop is best illustrated by examples.

(*a*) *The* 1967 *outbreak in Tamesna in northwest Niger*

Populations in the Sahara in the first half of 1967 consisted of isolated or scattered adults but included denser concentrations formed to the north and west of Ahaggar, where breeding began in March, following heavy February rains, Hoppers occurred at densities comparable with those found in gregarious populations, but although there was some marching, they were mainly solitaricolor.

In June there was a widespread southward movement and low-density adults appeared in south Algeria and northwest Niger. In addition a swarmlet measuring 42 ha and containing some 35000 individuals was seen on 25 June, in the midst of scattered night-flying populations spread between points over 260 km apart, and a few small groups were seen near the Niger-Algerian border in June and July. These assemblages apparently dispersed and there was no gregarious breeding reported anywhere in the Sahel zone of West Africa in July and August. There was, however, some local grouping of hoppers and control of resultant scattered adults in northeast Mali and in southwest Algeria.

In September and October, when low-density populations were widespread in West Africa, quite large numbers of scattered immature adults arrived in Tamesna from the Sahel, migrating at night and augmenting older remnants of populations which had arrived in June. Initially these immigrants were in the solitarious phase behaviourally and physiologically, while morphologically they were solitariform to low-transitiform.

Detailed observations (Roffey & Popov 1968) in Tamesna, where locally heavy rain fell in August, showed that locusts were appearing progressively further north and were practically confined to areas of developing vegetation, principally *Tribulus* and *Schouwia*. This suggested that the immigrants were selectively settling in such habitats, which occupied less than 10% of the area, and resulted in adult densities of up to 2000 ha^{-1}. The total population was estimated from ground and vehicle traverses at 5 million.

Concentration on the macro-scale was followed by concentration on the micro-scale as successive immigrant adults matured and searched for oviposition sites. This led to the formation of dense groups of egg pods of all ages. The densest group examined contained 71 pods in 900 cm^2, a density comparable with laying by swarms, and represented adult concentration by a factor of 4000000. The average number of eggs per pod was 133. As there was no egg parasitization or predation, few inviable eggs, and dissections suggested that each female probably laid three pods, the potential multiplication rate was approximately 200. By the end of October, however, when the median age was fourth instar, the population was estimated at 80 million. The actual multiplication was thus only 16-fold.

Gregarization was most pronounced in the hopper stage. Initially only one or two hoppers were present in individual plants but, as numbers increased, the formation of small roosting, basking and feeding groups was followed by the appearance of larger groups and ultimately of marching bands. The production of swarms was prevented by control.

(*b*) *The* 1973 *outbreak in the Indo-Pakistan summer breeding area*

Another example of the production of gregarious from low-density populations occurred in the Indo-Pakistan summer breeding area between July and November 1973. The case also shows that locusts involved in an outbreak may be derived from several sources and from more than one region. Thus the parent (F_0) generation probably comprised: (i) small numbers which had overwintered in Rajasthan from the previous season; (ii) larger numbers of scattered immigrants arriving from the west in April and May. These almost certainly originated in Red Sea coastal areas of Arabia (figure 1), where an earlier outbreak with concomitant gregarization occurred between November 1972 and March 1973, but swarm formation was prevented by control. Some of these locusts reached Afghanistan, others moved to Rajasthan, where estimated densities rose from 50 km^{-2} in April to 1275 km^{-2} in May (figure 1); (iii) further low-density immigrants arriving in July and August from Iran and Afghanistan.

Widespread laying by low-density F_0 adults commenced in Bikaner and Las Bela districts in

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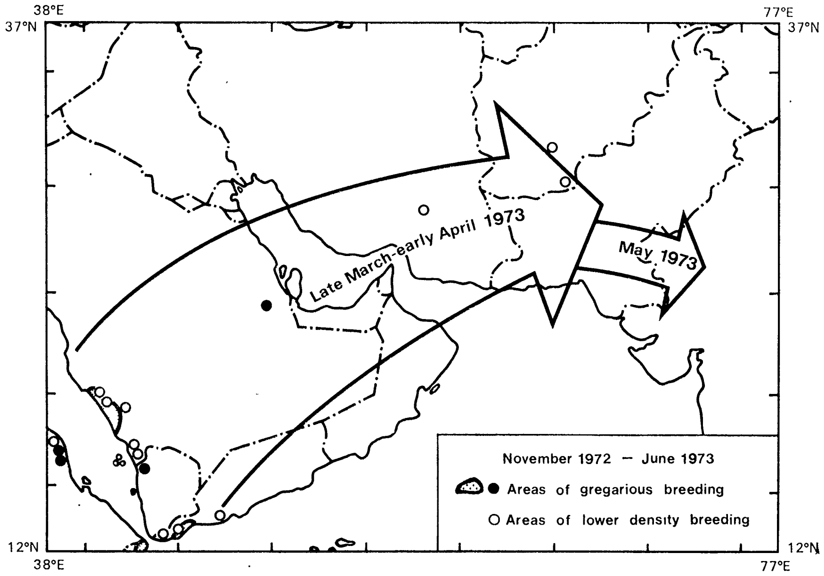

FIGURE 1. Winter-spring breeding areas in the central and eastern regions between November 1972 and June 1973, and eastward movement of adults, March–May 1973.

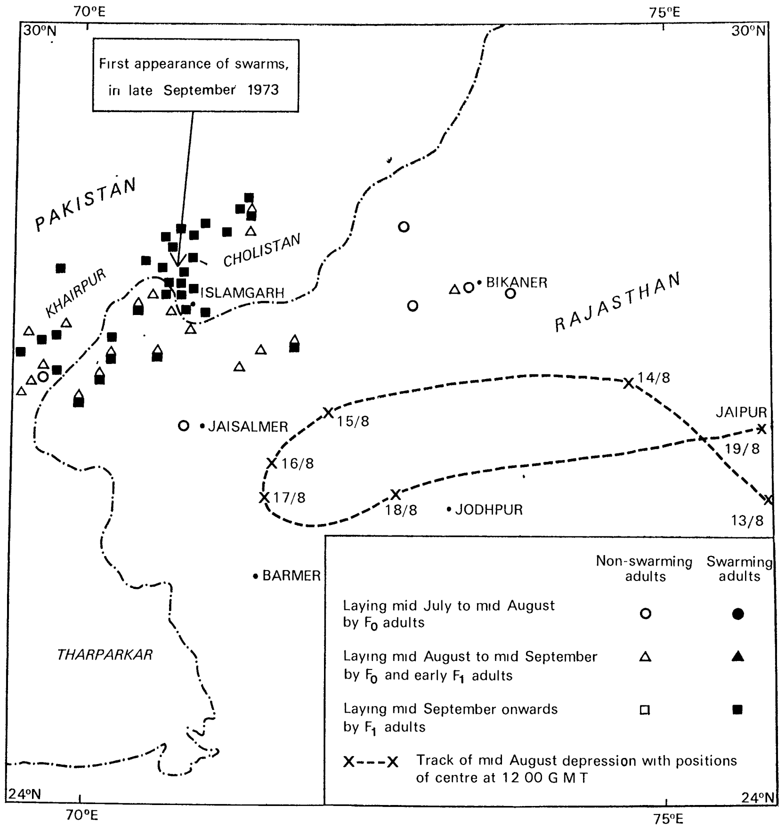

FIGURE 2. Monsoon laying in India and Pakistan, July–October 1973, and track of mid August depression.

mid-July following moderate rainfall, and in early August extended to west of Jaisalmer and the Tharparkar desert (figure 2). Adults of the F_1 generation began to appear in mid-August.

Between 13 and 19 August a slow-moving depression gave very heavy rainfall over west Rajasthan (figure 2). Renewed layings by surviving F_0 adults, augmented by late arrivals from the west and rapidly maturing early F_1 adults, started from about 23 August in areas 50–200 km west and north of the track of the depression. These produced numerous hopper bands of mixed instars, indicating successive layings, and immature swarms from mid October.

The first reports of swarms referred to copulating and laying swarms observed in late September near Islamgarh, some 100–200 km from the track of the mid August depression. These almost certainly consisted of F_1 generation adults which became concentrated as they matured and laid, though one immature swarm probably concentrated in the hopper stage. Successive layings by these swarms and by numerous scattered adults gave rise to many hopper bands, and many swarms appeared in November.

It appears that the persistent mid August depression did not concentrate adults directly, but that the latter became concentrated within areas providing exceptionally favourable breeding conditions, brought about by the rains associated with the depression and located at some distance from its track. In both Tamesna and Rajasthan the initial concentration of locusts was due not to low-level wind convergence, which has previously been considered an important concentrating factor (Rainey 1962), but to the behavioural responses of the locusts to the ground environment.

These examples demonstrate the importance of the concurrent and inter-related processes of concentration, multiplication and gregarization in Desert Locust outbreaks (Kennedy 1939, Roffey & Popov 1968). In the Tamesna case gregarization was mainly in the hopper stage; in 1973 in India swarms appeared among adults as they matured and bred. The first appearance of swarms when increasing adult populations reach sexual maturity is of interest and has been observed in several earlier outbreaks and upsurges in the Eastern Region, and in the Red Sea and Gulf of Aden areas; in summer 1974 it was seen in Mauritania (Skaf 1978). It is suggested that an important concentrating factor among adults which are increasing in density is the tendency of all phases to group when mating and laying (Roffey & Popov unpublished, Norris 1963). This may provide opportunities for mutual habituation among initially solitarious adults and account for the occurrence of swarms of sexually mature solitariform locusts, seen by, e.g. Kennedy (1939) and Ellis & Ashall (1957).

However, populations produced during outbreaks are often only partially gregarized. In the deep recession which extended over most of the area between 1963 and 1966, there were, with the exception of the populations produced in India and Pakistan in 1964, few fully confirmed reports of bands and swarms, and such populations differed qualitatively and quantitatively from those characteristic of plagues. In no case did bands persist through all instars; if bands were present in the first instar they were controlled or they dissociated, more often it appears that they only formed in the middle–late instars, and sometimes dispersed on fledging. Even when locusts left their source areas as groups or swarms they apparently often failed to remain cohesive during their migration to the next breeding area. This is strongly suggested by the complete failure of intensive aerial searches to find again any of the swarms reported by ground observers in the manner regularly achieved during plagues. For example, in the plague year of 1959, 169 sightings of swarms were made in 127 flights over the northern Somali peninsula in July–September, when swarms are regularly concentrated there in a narrow belt during plagues.

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By contrast no swarms were sighted during 120 h of flying in 1964 and 116 h in 1965, in the same area and season.

The swarms were also smaller in size and density and therefore in locust numbers. The largest swarm during 1963–7 for which quantitative data exist was 3.7 km^2 and contained 2.5–3 million locusts; these figures contrast with swarms characteristic of plagues which are frequently tens and sometimes hundreds of square kilometres in extent and contain 20–150 million locusts per square kilometre (Joyce 1962). On the other hand some low-density populations were estimated to have contained tens of millions of adults and were thus an order of magnitude larger numerically than the largest swarm reported in the recession (Roffey, Popov & Hemming 1970).

Evidence from the current recession (1969 to late 1976) provides some interesting contrasts with the earlier one. After a period of 7 months from November 1971 to May 1972, when no gregarious populations were reported, population levels in the Central and Eastern Regions were considerably higher than in 1963–6. These larger populations originated in 1972 in northern Somalia and Oman from initially low-density populations. In both areas heavy rains fell between January and April, and hopper bands appeared in the spring. Subsequently hopper bands and swarms were reported in one part or another of the summer and winter-spring breeding areas in each year till 1976. Although some swarms were exceptionally large for recession periods they still differed in several respects from those during plagues. Throughout this period they remained within the limits of the recession area. There was only one instance (October–November 1973 in the Eastern Region) when the bulk of the population emigrated from its source area as day-flying swarms. In spite of some reports of swarms on probable migration routes, locusts frequently arrived at their breeding sites at low densities. Thus during the period 1972 to mid 1974, which was examined in greater detail, important infestations occurred in 14 seasonal breeding areas. In seven of these areas the parent generation had moved in and bred as low-density populations; in another four the parent generation included some mature swarms, almost certainly formed at the onset of breeding in two cases, and possibly in all four; in three areas the parents arrived as immature swarms. Thus in only a small proportion of cases were locusts likely to have migrated from their source to their breeding areas as swarms.

While control must have reduced the numbers of locusts, their failure to develop into a full plague may have been due to the absence of the requisite rainfall conditions (Pedgley, this symposium, § 2).

4. Characteristics of plague upsurges

Plague upsurges will now be considered, taking as an example the main events in the Central Region in 1967–8; the account is largely based on analyses by Pedgley & Symmons (1968) and Bennett (1976).

In the first half of 1967 the situation appeared to be unexceptional. Reports of unconfirmed swarms on the Somali peninsula and in Jordan in the 1966–7 season could not be substantiated; an infestation by grouped hoppers in southeastern U.A.R. in May gave rise to a large population of scattered adults. But the sequence of events leading to the upsurge may have already started in unsurveyed parts of the Arabian peninsula. In November 1966 a tropical cyclone brought heavy rains to parts of southern Arabia; in March–April 1967 abundant rains fell over most of the southern half of Arabia during the passage of deep troughs in upper westerlies; in July more heavy rain fell in south Arabia during an unusual monsoon disturbance. This sequence of rains would have provided locusts with favourable breeding conditions through at least three generations, and information obtained subsequently indicated that very large numbers of locusts had been present in Oman by the autumn of 1967, and had been gregarizing (Popov 1968). It is likely that some building up of populations occurred also in inner southwest Arabia, where good rains fell in March–May and July. To the west of the Red Sea, an infestation by gregarizing hoppers occurred in October–November over a limited area in interior Sudan; any escapes from that area probably moved to the coast (figure 3).

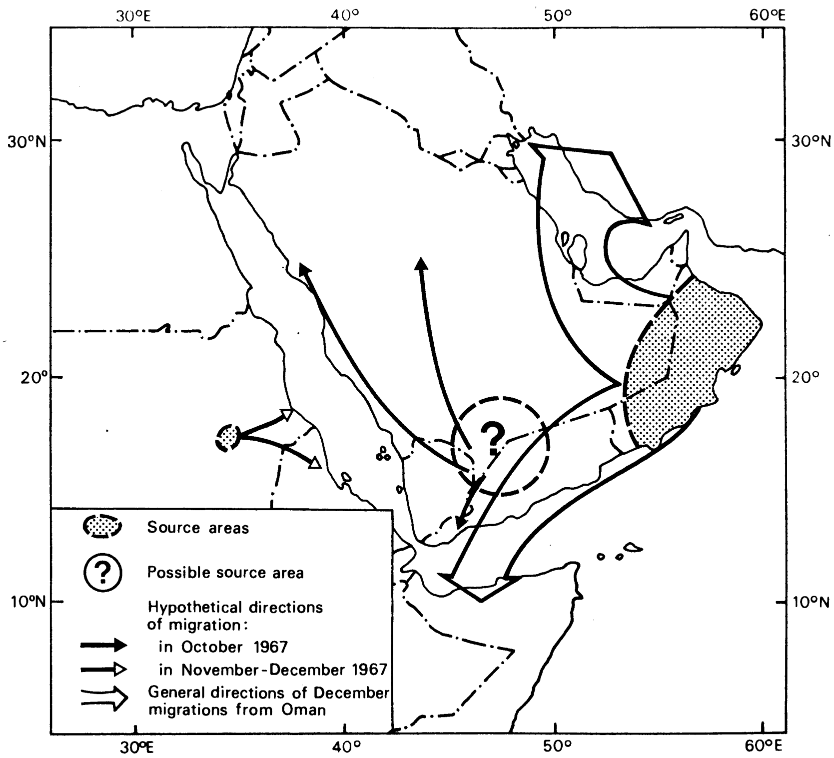

Figure 3. Spread of Desert Locust populations in the last quarter of 1967.

In October 1967 some of the locusts produced in southern Arabia spread to western and southwestern coastal areas and to interior Saudi Arabia (figure 3). Most were solitariform and scattered, but the appearance of groups in South Yemen and of a swarmlet with gregariform morphometrics at Najran (south Asir) (figure 5) indicated the presence in the populations of some gregarized components. Then in December swarms of transitiform locusts crossed from Oman to the coast of the Somali Republic. Other swarms moved north and east and initiated the upsurge in the Eastern Region by invading Iran (figure 3).

The 1967–8 season was again marked by several spaced-out periods of heavy rains, viz. in the Red Sea and Western Gulf of Aden areas in November and in February, and in coastal and interior Saudi Arabia in April–May. As a result, locust populations in Arabia and neighbouring countries were again provided with very favourable breeding conditions through several generations.

Breeding by gregarizing local populations and by invading swarms continued on the northwest coast of the Somali Republic through the winter and spring (figure 4) and resulted in the production of a considerable number of swarms by late April–May. Similarly breeding and gregarization took place in winter and spring on both coasts of the Red Sea, but was effectively controlled on the African side. On the Arabian coast, where locusts passed through at least three, and possibly four, generations by May–June, breeding gave rise to numbers of swarms. In addition groups and swarms moved in mid March from the coast to central and north Saudi Arabia and bred there (figure 4). Their progeny formed swarms between May and July.

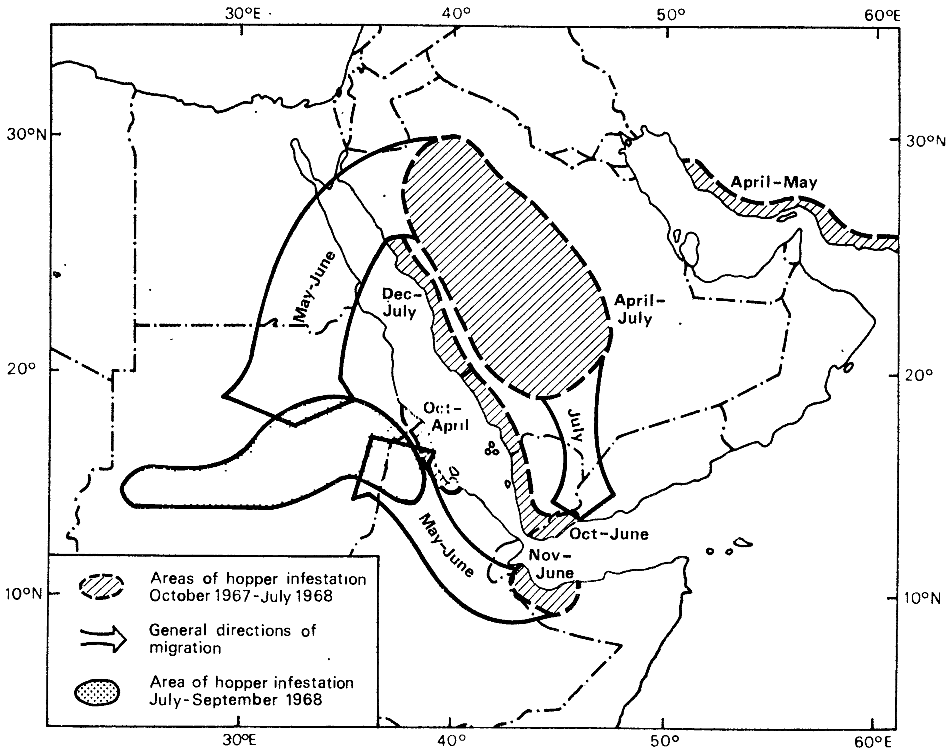

Figure 4. Areas of hopper infestations in the 1967–8 season and spread of Desert Locust swarms to summer breeding areas in 1968.

In May and June 1968 swarms moved out from the northwest Somali peninsula and Arabia, and converged in the summer breeding areas in north Ethiopia and Sudan, where breeding commenced in July (figure 4); from Sudan some of the Arabian swarms moved west to Niger and Mali, and probably Mauritania. New swarms appeared in Sudan in September and some of them spread to the Western Region, reaching Morocco in October 1968.

During the 1967–8 season the proportions of swarming locusts in the Central Region apparently increased from generation to generation, and populations which emigrated to north Ethiopia and Sudan from the Somali peninsula and Arabia moved out as gregarious swarms. Their morphometrics, however, were still far from extreme *gregaria* (figure 5, populations 4 and 5), and these were not attained until locusts had passed through one more generation (figure 5, population 6) conservatively estimated as *at least* the fourth in the gregarizing sequence.

The outstanding features of the plague upsurge were: (*a*) repeated occurrences of widespread heavy rains, falling at appropriate intervals for successful breeding by several successive generations in areas connected by locust movements; (*b*) the resultant building up and

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concomitant gregarization of locust populations culminating in the production of large numbers of cohesive gregarious swarms. Earlier plague upsurges have been similarly associated with repeated occurrences of heavy and widespread rains. Thus, during the 1948–9 plague upsurge, the occurrence in spring 1949 of large scattered populations and swarms on Oman was preceded by widespread torrential rains brought to southeast Arabia by a tropical cyclone in October 1948, and by further heavy rains on the eastern edges of the Rub al Khali in December and March. During the same season some partial gregarization of hoppers occurred in the spring breeding areas of Pakistan, where swarm formation was prevented by control, and possibly in southeast Iran, where a group was seen in April. In May–July some of the Oman

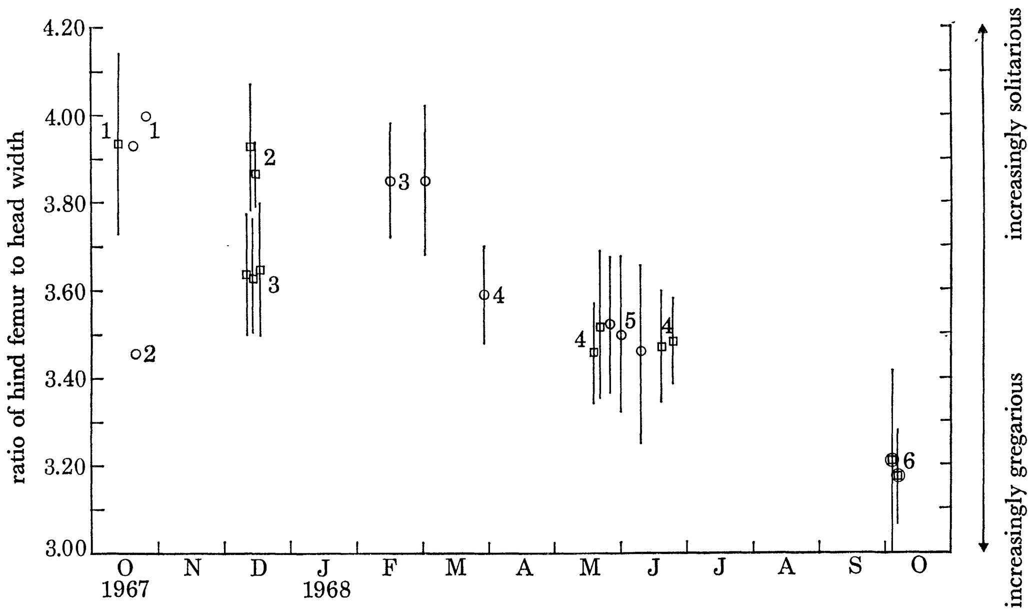

FIGURE 5. Morphometrics of the 1967–8 upsurge populations. The values plotted against the ordinate are the means and standard deviations of the ratio (length of hind femur)/(width of head capsule) of males, taken from successive generations of populations in two sequences. □, populations in sequence 1; ○, populations in sequence 2.

sequence 1 (□)

1 NW Somali coast F_0
2 NW Somali coast local F_1
3 NW Somali coast immigrants F_0
4 Eritrea, immigrants from NW Somali coast F_2+F_3

sequence 2 (○)

1 Tihama F_0 } Saudi Arabia
2 Najran F_0 } Saudi Arabia
3 Tihama F_1 } Saudi Arabia
4 Tihama F_2 } Saudi Arabia
5 Egypt, immigrants from Arabia F_3
6 Niger, immigrants from Sudan F_4 (sequence 2) and F_3+F_4 (sequence 1)

populations moved to the Indo-Pakistan summer breeding areas, greatly augmenting the locusts reaching them from Iran and Pakistan. All the immigrant populations arrived in scattered formations. The 1949 monsoon rains enabled them to pass rapidly through two to three generations and give rise to numerous swarms. Yet another example is provided by an upsurge in the Western Region in 1941, which followed the build-up and gregarization of locust populations in association with extensive flooding in many parts of the Sahara between September 1940 and May 1941 (Waloff 1966, 1972).

5. Conclusions and practical implications

We must now recapitulate those features of Desert Locust bionomics which have practical implications for the strategy of outbreak and plague prevention.

All field evidence points to the great instability of recession populations and the ease with which they may partly gregarize, and then disperse again. Even the largest recession populations appear to be qualitatively different from those characteristic of plagues. In particular, recession swarms are unstable and rarely remain cohesive during migration. They are also quantitatively different from plague swarms and may comprise only an insignificant proportion of regional populations. It follows that control strategy evolved during plagues which is based on the discovery and destruction from aircraft of cohesive swarms may be largely inapplicable to recession populations, and to the prevention of outbreaks and plagues.

Outbreaks develop through concentration, multiplication and gregarization. An essential requirement for an outbreak is abundant rainfall, often itself associated with convergent airflow which may concentrate locusts. Plague upsurges depend on similar processes but occurring on a larger scale, with a sequence of widespread rains falling in complementary areas and providing conditions for rapid multiplication and gregarization through several successive generations.

The prevention of outbreaks and plagues calls for a strategy which takes advantage of situations in which recession populations are most likely to be concentrated by environmental factors and their own behaviour. This requires the timely identification of areas where good rains have fallen and where locusts are breeding, and the application of prophylactic control measures against any dangerously large and concentrated populations, aimed at the destruction of parents, nymphs and fledglings before the new generation leaves its source area.

Since plague upsurges have been shown to occur at irregular intervals (Waloff 1976), and sequences of heavy and widespread rainfall cannot yet be predicted (Winstanley 1973), it will be necessary to identify the potential breeding sites on a continuing basis.

The practice of seasonal surveys based on the knowledge of broad seasonal changes in the distribution of recession populations, aimed at discovery of breeding areas and control of dangerous populations in them, has been adopted by all Desert Locust control organizations. In West Africa, in particular, the technique of sequential aerial and ground surveys ensures rapid and efficient detection of locust populations by location of suitable habitats from the air followed by inspection from the ground. It is also in West Africa that advances have been made in identifying the types of locust habitats, in which, given rain, outbreak conditions are liable to occur.

Despite these advances, the practical difficulties of keeping the Desert Locust in recession are very great; the recession area is immense and over much of it the rainfall and locust appearances are sporadic. Even in areas with more regular seasonal rainfall not all dangerous population increases and cases of gregarization are detected in time, while extensive areas of sporadic rainfall, known to have been sources of upsurge populations, remain entirely unsurveyed. There is a pressing need to improve the survey coverage and to facilitate it by the application of more modern techniques.

In the first place, more could be achieved by closer and more immediate links between locust survey organizations and local meteorological services. In areas where an association between mobile depressions and concentration of breeding locusts is suspected, current meteorological charts could provide valuable guidance for locust surveys. Again, in view of the importance in the last two upsurges of widespread and heavy rains falling in Arabia and neighbouring areas, in association with tropical cyclones or with slow-moving troughs in the upper westerlies, it is essential for the locust monitoring and control organizations to be aware of such meteorological events *as they occur*.

Recent developments in the use of ground and airborne radar provide a valuable tool with which to monitor airborne locusts, particularly during recessions, when most adult populations are likely to fly by night.

An interesting recent development is the experimentation in the use of satellite imagery for detecting locust breeding sites. In 1973 C.O.P.R. staff undertook a comparison of ERTS 1 imagery with the actual distribution of moist soil and vegetation of the Red Sea coast of Saudi Arabia, and proved the feasibility of detecting suitable breeding sites (Pedgley 1974). More recent studies by the FAO Remote Sensing Unit at a test site in Algerian Sahara indicate that meteorological satellite imagery is likely to provide information on rainfall amount, distribution and timing, and there are plans to extend this work to cover the whole Desert Locust area (Hielkema & Howard 1976). Provided the problems of the rapid analysis of imagery and of communication and timely requisite action can be solved the development of this method promises a hopeful approach to the intractable problem of adequate survey and preventive control over the entire recession area.

However, the monitoring of the satellite imagery must obviously be done hand in hand with the monitoring and assessment of current Desert Locust situations. In view of the known ability of Desert Locusts to move over great distances and from region to region, the proper assessment will be achieved only if information from the whole Desert Locust area is assembled and critically analysed at a single centre where an overall view can be taken.

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