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Continuity in Major Populations of Migrant Pests: the Desert Locust and the African Armyworm

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PROBLEMS OF ALTERNATIVE HYPOTHESES

Continuity in major populations of migrant pests: the Desert Locust and the African armyworm

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[Pullout 1]

For both these pests, the records of their occurrences in damaging high densities are envisaged not as relating to many different and independent populations, but as intermittent contacts with varying fractions of successive generations of the highly mobile and fluctuating regional populations: recognized continuously for the Desert Locust, and for the African armyworm over successions of up to seven generations during eight to eleven months in a year and in most years. Each report of a high-density population would accordingly help to provide warning of where and when the next might be expected. Furthermore, on this hypothesis control operations against each generation could be hoped to contribute to reducing the scale of operations needed against the next generation, in a potentially cumulative manner.

1. Introduction

The Desert Locust (*Schistocerca gregaria* Forsk.) and the African armyworm (*Spodoptera exempta* Walker), though very different insects, both show striking differences in behaviour (and also in colour) between solitary-living, relatively less mobile populations with green nymphs or larvae, and high-density, more mobile populations with characteristic black patterns in the immature stages. Attention was drawn to this remarkable analogy many years ago, in the classical Phase Theory of Uvarov (1921, 1966, 1977) and Faure (1923, 1943); and for each of these pests there are analogous alternative hypotheses concerning the significance or otherwise of these phase-differences in relation to the dramatic fluctuations in local numbers which are so characteristic of the attacks of both species.

For certain other locusts, particularly *Locusta* and *Nomadacris*, more than 40 years of experience have largely endorsed the original idea that the change from the solitary-living to the gregarious phase, the process of gregarization, accompanies the great increase in numbers and densities during the development of a new plague.

The process of gregarization is now commonly seen as an essential aspect of the development of a plague of the Desert Locust also, and Chris Hemming and his co-authors (this symposium) provide an up-to-date and authoritative presentation of this point of view, followed at their suggestion by an account by David Pedgley of some of the weather factors involved. Derek Rose presents a somewhat analogous point of view in respect of armyworm, similarly based on many years of experience of this pest in the field.

A few of us however interpret the very extensive, but still characteristically incomplete, evidence now available on the attacks of the Desert Locust and the African armyworm very differently. We envisage that populations exhibiting high densities (intermittently or continuously) are always (Desert Locust) or regularly (armyworm) to be found, and that both

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species regularly undertake long-distance migrations, not only when populations are generally large but also when they are small. This view-point has developed primarily from detailed mapping and biogeographical analyses of the very striking changes in space and time of the attacks of these pests, particularly for the purpose of forecasting (with verification, and largely unpublished), and also from field experience of flight behaviour.

2. The desert locust

The biogeographical approach has already been briefly illustrated in our findings on the Desert Locust decline of the 1960s (Rainey, Betts & Lumley, this symposium, §§ 2*e* and 3), when we were unexpectedly faced with the quite new problem of maintaining, under recession conditions, the regular Desert Locust forecasting service of those days to the 40-odd countries concerned.

(*a*) *Outline of a recession: treatment of data*

In 1967 Gurdas Singh, then FAO Desert Locust specialist, requested from us a list of the most important locust populations which had been recorded since the onset of the recession period in 1963 (Singh 1967). This posed the crucial question of which had in fact been the most important populations; in the event, three straightforward criteria were found to provide a list sufficiently comprehensive to include every recorded population which there was any reason to suspect, from any point of view and with the full benefit of hindsight, of having perhaps been important in subsequent developments. These three criteria were:

(i) Reports of locust populations against which *control measures* were undertaken, because such expenditure of resources will have reflected a degree of concern, from local experience, on the part of the control organizations responsible.

(ii) Reports of *gregarious populations* (swarms of adults or bands of nymphs), with some supporting evidence, such as: (*a*) subsequent observations of the presence of locusts in numbers, or of exuviae or excreta; (*b*) other independent reports of gregarious populations from the same area and period (isolated reports of swarms or bands, without such supporting evidence, were omitted); or (*c*) other reports at appropriate times and places to represent potential parents or progeny of the locusts under consideration.†

(iii) Other reports of locusts, not in swarms or bands and with no control attempted, but included either because of recorded scale – with evidence of locust numbers of the order of millions – or again because of their relationship in space and time† to other infestations or to weather-systems.

Reports separated by less than a month in time and by less than 500 km in distance were grouped for convenience into a single entry.

After the list had been compiled and mapped (figure 1), a diagram (figure 2, pullout 1) was devised to facilitate the systematic and comprehensive consideration of the relation of these reports in time and space, and to help in maintaining the vital distinction between observation and inference. The diagram uses time and geographical longitude as axes, foregoing the coordinate of latitude (and varying the scale of longitude to save space). It illustrates the possibilities of inferring links between these reports, of the kind which we had automatically continued to

† In the event, consideration of relations in time and space was necessary for the inclusion of only two (C18 and E12) of the resulting total list of 50 separate groups of reports (appendix) and omission of these two would make no difference to the conclusions we suggest.

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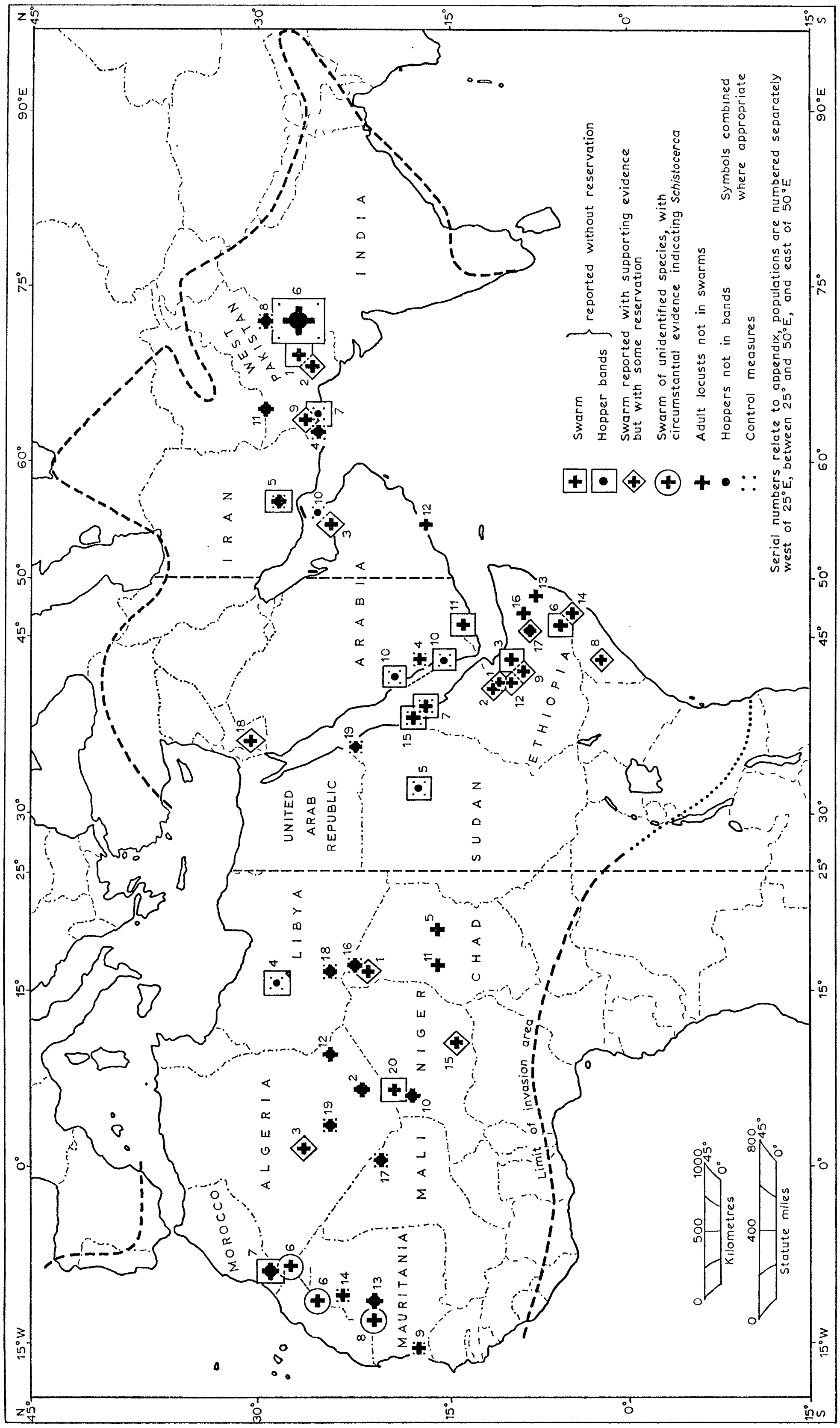

FIGURE 1. Map of main Desert Locust populations, 1963–7.

envisage from 1960 onwards, at the start of the recession, in the hope that such links might help us with the new problem of forecasting at low overall levels of locust populations; the dotted lines show potential migration routes, for which events in earlier years have provided evidence of a precedent for migrations across the area and at the time of year under consideration. A limited selection of other reports of locusts in small numbers, not satisfying criteria (i) to (iii), has also been shown in figure 2, both as supplementary circumstantial evidence of some of the links envisaged, and as illustrating the evidence for continued seasonal movements even with populations at very low levels (e.g. India and Pakistan 1966–7).

As guidance on such potential links we had the very considerable body of information on migration routes, over distances frequently of the order of thousands of kilometres per month, provided in particular by the Anti-Locust Research Centre's 40 years of maps and analyses of current Desert Locust information. These included evidence from many 'natural experiments' in which population movements could be recognized across areas previously clear (e.g. fig. 2 in Rainey 1974; fig. 6.2 in Betts 1976). Many of these migration routes had been followed with a very striking degree of seasonal regularity, as illustrated by the autumn invasion of Morocco (Rainey, Betts & Lumley, § 3*a*) and precedents were usually available even for the most rarely followed routes. Thus for example recorded Desert Locust history was already so extensive by 1960 that during the following 6 years, when 48 different countries were invaded, many of them repeatedly, these invasions did not include a single case of swarms arriving in a manner without recorded precedent in the area and at the time of year concerned. We knew also that even solitary-living Desert Locusts could be expected to show geographical patterns of migration with considerable similarities to those of the swarms though on a rather smaller scale, as first found by Rao (1942) and as already mentioned by M. Abdallahi (this symposium, § 2*b*). Furthermore, radar observations in the southern Sahara have provided striking evidence of night-flying Desert Locusts at low densities travelling at ground-speeds of more than 60 km/h and heights up to 1800 m (Schaefer 1976).

(*b*) *Outline of a recession: findings*

These links indicate how each one of our 50 reports could be regarded as circumstantial evidence of the antecedents of a later reported population: with the two reports thus capable of being interpreted as sampling successively (and to varying extents) either the same population or its progeny. The finding we would particularly emphasize is that all but four of the 50 populations listed could indeed be derived, by such recognized migration-routes, from a potential parent population of which at least some part had already been reported and included in our list, or from known earlier gregarious populations of 1963.

On the other hand, the remaining four, for which no such links could be suggested, must have resulted from undetected breeding (and possible gregarization) somewhere on the fringes of the Sahara during 1963 or early 1964, perhaps following an earlier move from the east; for the preceding $2\frac{1}{4}$ year gap was one of the longest breaks on record in the sequence of gregarious populations affecting a major region of the invasion area (Betts, in Rainey 1971).

This was the only such break found in the diagram. Moreover some of the gregarious populations of the 1968 upsurge could be connected with some at the end of the preceding plague period, in 1963, by sequences of successive generations of fully confirmed gregarious populations separated by gaps of no more than 18 months. Furthermore these gaps were potentially bridged by reports, with some supporting evidence, of locusts showing at least some degree of gregarious

FIGURE 2. Desert Locust recession and upsurge 1963–8: a preliminary outline. Main reported locust populations indicated by |framed| locality names in appropriate month(s) and at approximate longitudes, numbered to correspond with lists in the appendix and |underlined| if control measures undertaken; reports of gregarious populations (swarms of adults or bands of nymphs) in |CAPITALS|, those of locusts not in swarms or bands in |lower case|. Limited selection of other locust reports shown by unframed locality names, e.g. Hargeisa.

The original list and diagram included reports up to May 1967, and were completed in September 1967, very shortly before the upsurge became apparent. The diagram was later extended to July 1968, to cover the upsurge, but no amendments were made – or needed – in the continuing links which had been inferred earlier.

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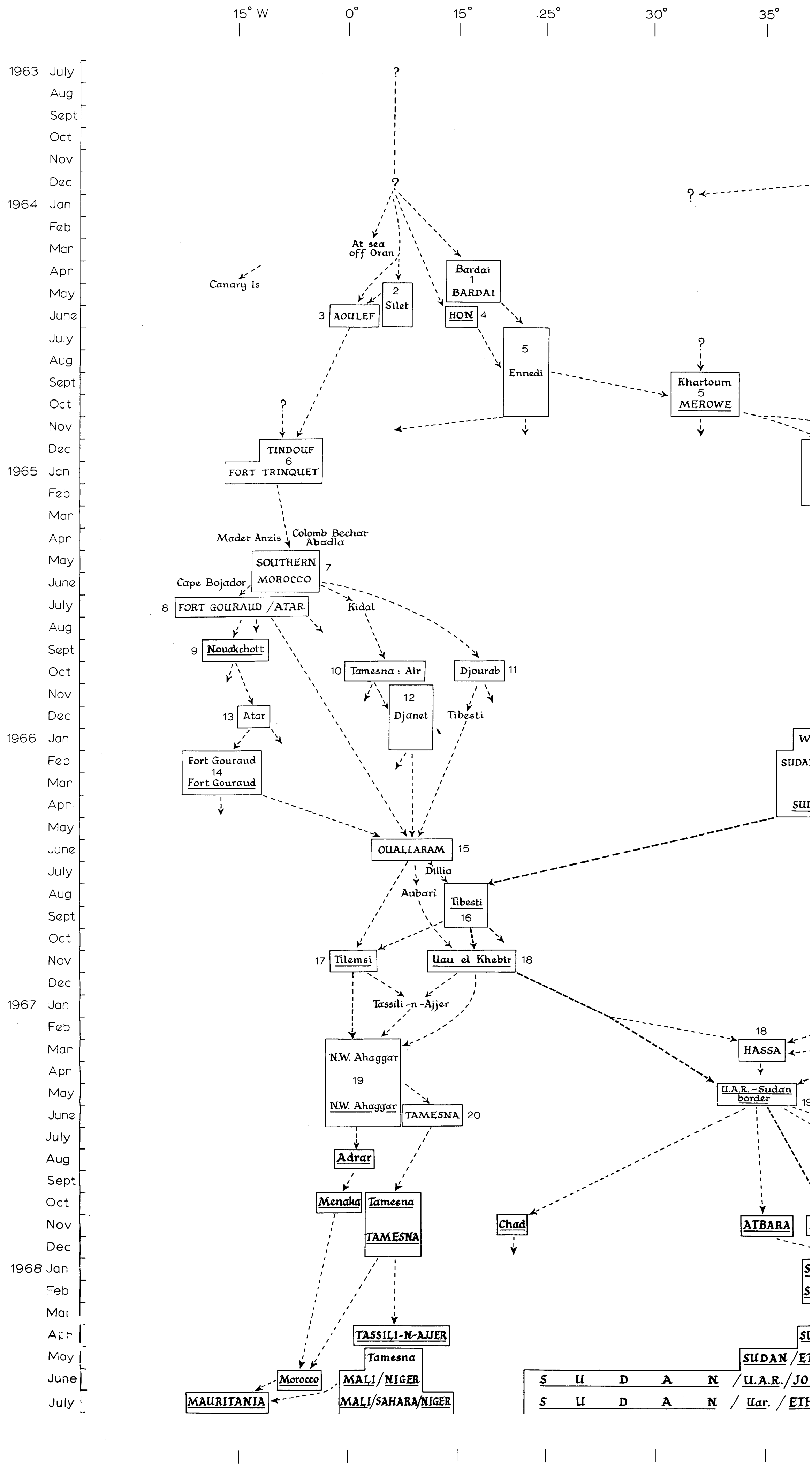

15° W
0°
15°
25°
30°
35°
1963 July
Aug
Sept
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Nov
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1964 Jan
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Mar
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May
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1965 Jan
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1966 Jan
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1967 Jan
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Mar
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June
July
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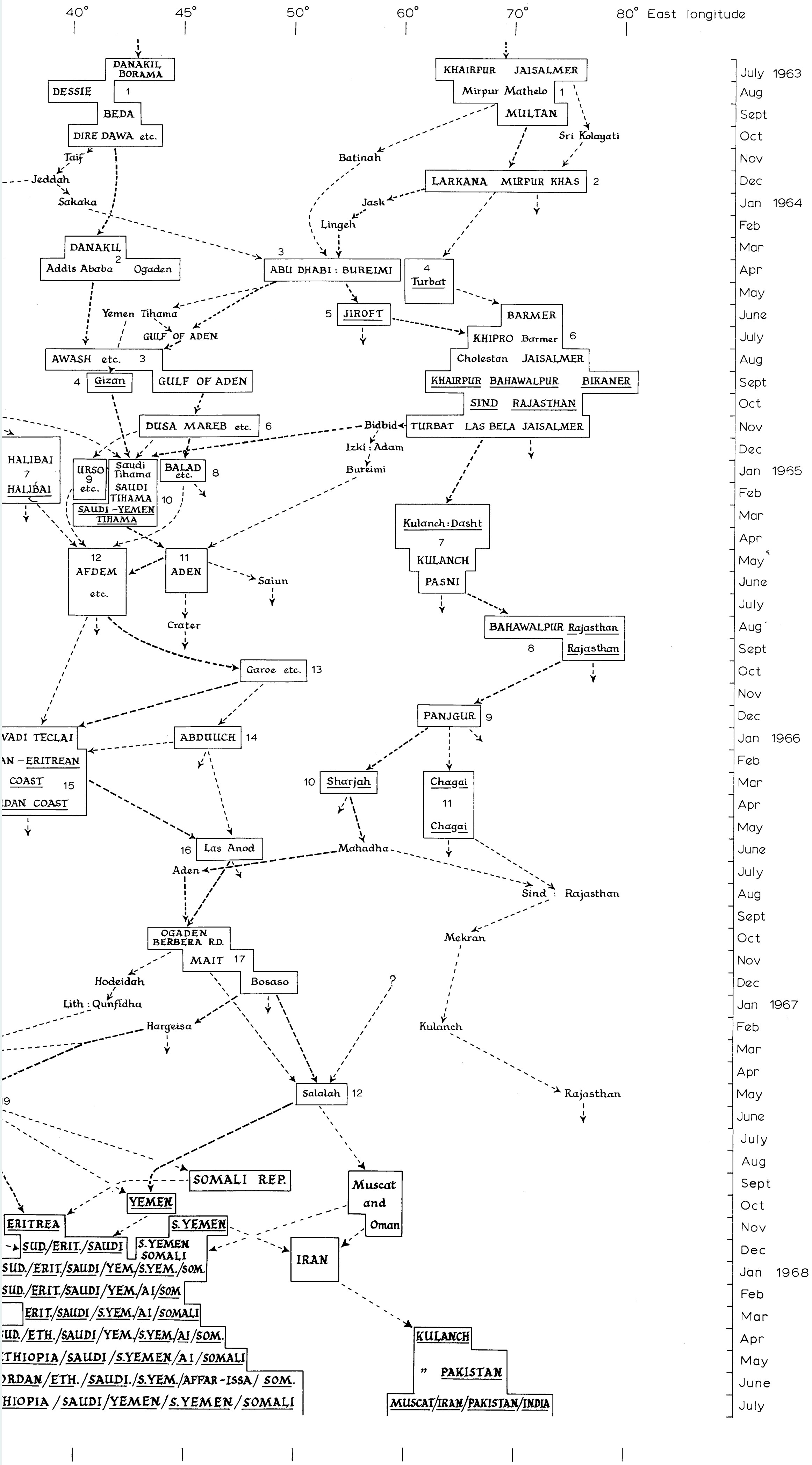
Oct
Nov
Dec
1968 Jan
Feb
Mar
Apr
May
June
July
?
At sea off Oran
Canary Is
Bardai 1 BARDAI
2 Silet
3 AOULEF
HON 4
5 Ennedi
Khartoum 5 MEROWE
TINDOUF 6 FORT TRINQUET
Mader Anzis
Colomb Bechar Abadla
SOUTHERN MOROCCO 7
Cape Bojador
8 FORT GOURAUD / ATAR
Kidal
9 Nouakchott
10 Tamesna : Air
Djourab 11
12 Djanet
Tibesti
13 Atar
Fort Gouraud 14 Fort Gouraud
OUALLARAM 15
Dillia
Aubari
Tibesti 16
17 Tilemsi
Uau el Khebir 18
Tassili-n-Ajjer
N.W. Ahaggar 19 N.W. Ahaggar
TAMESNA 20
18 HASSA
U.A.R.-Sudan border
Adrar
Menaka
Tamesna TAMESNA
Chad
ATBARA
TASSILI-N-AJJER
Tamesna
Morocco
MALI/NIGER
MALI/SAHARA/NIGER
MAURITANIA
SUDAN
S U D A N / U.A.R.
S U D A N / Uar.



40°
45°
50°
60°
70°
80° East longitude
DANAKIL BORAMA
DESSIE
1
BEDA
DIRE DAWA etc.
Taif
Jeddah
Sakaka
DANAKIL
2
Addis Ababa
Ogaden
KHAIRPUR JAISALMER
Mirpur Mathelo
1
MULTAN
Sri Kolayati
Batinah
LARKANA MIRPUR KHAS
2
Jask
Lingeh
3
ABU DHABI : BUREIMI
4
Turbat
5
JIROFT
BARMER
KHIPRO Barmer
6
Cholestan JAISALMER
KHAIRPUR BAHAWALPUR BIKANER
SIND RAJASTHAN
Bidbid
TURBAT LAS BELA JAISALMER
Izki : Adam
Bureimi
Yemen Tihama
GULF OF ADEN
AWASH etc.
3
4
Gizan
GULF OF ADEN
DUSA MAREB etc.
6
HALIBAI
7
HALIBAI
URSO
9
etc.
Saudi Tihama
SAUDI TIHAMA
SAUDI-YEMEN TIHAMA
BALAD etc.
8
10
12
AFDEM
etc.
11
ADEN
Saiun
Crater
Kulanch : Dasht
7
KULANCH
PASNI
BAHAWALPUR Rajasthan
8
Rajasthan
Garoe etc.
13
PANJGUR
9
WADI TECLAI
AN-ERITREAN
COAST
15
DAN COAST
ABDUUCH
14
10
Sharjah
Chagai
11
Chagai
16
Las Anod
Mahadha
Aden
Sind : Rajasthan
OGADEN BERBERA RD.
MAIT
17
Bosaso
Mekran
Hodeidah
Lith : Qunfidha
Hargeisa
?
Kulanch
Salalah
12
Rajasthan
19
SOMALI REP.
YEMEN
Muscat and Oman
ERITREA
S. YEMEN
SUD./ERIT./SAUDI
S. YEMEN SOMALI
SUD./ERIT./SAUDI/YEM./S.YEM./SOM.
SUD./ERIT./SAUDI/YEM./AI/SOM.
ERIT./SAUDI/S.YEM./AI/SOMALI
SUD./ETH./SAUDI/YEM./S.YEM./AI/SOM.
ETHIOPIA/SAUDI/S.YEMEN/AI/SOMALI
ORDAN/ETH./SAUDI./S.YEM./AFFAR-ISSA/ SOM.
HIOPIA / SAUDI / YEMEN / S.YEMEN / SOMALI
IRAN
KULANCH
" PAKISTAN
MUSCAT/IRAN/PAKISTAN/INDIA
July 1963
Aug
Sept
Oct
Nov
Dec
Jan 1964
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct
Nov
Dec
Jan 1965
Feb
Mar
Apr
May
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July
Aug
Sept
Oct
Nov
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Jan 1966
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Mar
Apr
May
June
July
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Sept
Oct
Nov
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Jan 1967
Feb
Mar
Apr
May
June
July
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Sept
Oct
Nov
Dec
Jan 1968
Feb
Mar
Apr
May
June
July

behaviour, so located in space and time as to bring the longest remaining gap down to 6 months. This finding also was reported at the 1968 Congress (Rainey 1971), but has been disregarded in subsequent work (Roffey, Popov & Hemming 1970); Bennett 1974, 1975, 1976), in which possibilities of connections between the gregarious populations of 1963 and those of 1968 have been rejected without indication of any study sufficiently comprehensive to have actually tested such potential connections. Figure 2 indeed suggests two such connecting sequences throughout 1963–8, indicated by the bolder dashed lines, providing a double bridge across the recession gap. At an early stage in this recession, it was pointed out that there had been no period free of reports of swarms or hopper bands somewhere in the Desert Locust area for longer than 4 months since 1935; that generalization was ventured 12 years ago, and, apart from a 7 month gap in 1971–2, it remains true in 1977. Furthermore, not since 1887 has there been a complete year without evidence of Desert Locust swarms somewhere (Waloff 1976).

(*c*) *Interpretation and discussion of findings*

The interpretation of these findings involves taking account of experience on a number of points. First there are the gaps of weeks and sometimes months which regularly occur in the reporting of known swarms even during plague periods, such as in southern Ethiopia during February/May. Then there has been personal experience (R.C.R.) of the occasional failure to find known swarms, even by aircraft and during plague periods, in particular circumstances paralleling in several respects those of some abortive searches during recession periods (Rainey 1963*a*, 1972*b*, and unpublished). Thus in mountainous terrain one small swarm could not be found again during extended search although it had been seen only hours earlier by the same highly experienced pilot (L.M.) and his observer, in the Usambara foothills in Tanzania on 4 March 1955. Again, in mid-1968 a much larger swarm, tens of square kilometres in extent, was found one evening among the Eritrean mountains near Barentu, but could not be found again next morning in an air search of an hour or so by the highly experienced pilot (A.W.) and observer of the previous evening. In other cases, marked reduction of locust flight activity was associated with air temperatures above 40°, both in northern Sudan in June 1953 and in northern Somalia in August 1957, which is consistent with laboratory evidence on the upper limiting temperature for sustained flight (Weis-Fogh 1956). Such temperatures may sometimes account for an absence of reports of day flight by swarms at high temperatures elsewhere.

Furthermore, a flying swarm can traverse even thorn-bush vegetation leaving practically no stragglers to be found only an hour or two later, thus providing no evidence of its passage (Rainey 1962). Again, on the crucial point (Gunn 1960) of locust numbers: a single square kilometre of swarm at a representative density (Rainey, Betts & Lumley, § 2*a*) of 50 locusts per square metre comprises 50 million locusts, sufficient either to cover an area of 2500 km^2 at the density which is for example routinely recorded on locust surveys in India and Pakistan as ‘countless’ ($>$ 20000 km^{-2}), or alternatively to provide one or two scattered locusts for every square kilometre over the entire invasion area of the species, from Assam to the Atlantic. Even a single small swarm can thus be quantitatively equivalent to an exceptionally numerous population of solitary-living locusts, of which the largest numbers indeed appear to occur as a result of temporary dissociation of swarms. Furthermore, for many individual months of a recession the few locusts reported cannot be regarded as representative of the much larger numbers which were clearly present a month or so previously and again a month or so later.

With these points in mind, it is suggested from figure 1 that even during the 1963–7 recession

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there does not appear to have been any period as long as a generation (say 3 months) over which the majority of Desert Locusts were at all likely to have been at low densities. Even during such a long recession, the available reports of gregarious locusts continued to provide a coherent and reasonable story, and the diagram directs attention to a number of reports (not only of swarms) (e.g. W15; C17) whose relations and even existence have been omitted from what has so far been published on the locust history of this period. More generally, we would suggest that while many and perhaps most Desert Locusts experience temporary periods at low density, e.g. after fledging, a majority of the species is usually and perhaps always to be found at high density, and that the larger low-density populations appear as a result of temporary dissociation of locusts previously and subsequently at high densities.

From earlier observations of both locust behaviour and morphometrics, it had been concluded (Rainey 1962) that 'the Desert Locust populations of a period of recession such as 1949 may differ from those of plague periods such as 1951, in numbers rather than in kind . . . Swarms both of (morphometrically) gregariform and of solitariform locusts were in fact recorded in each of the years 1949, 1950 and 1951'. Further evidence of apparently typical gregarious behaviour continued to accumulate during the 1963–7 recession, illustrated by well-documented cases in every year, e.g. reference numbers E6 (1964); C10 (1965); C15 (1966) in the appendix. Furthermore, on morphometrics, both recessions even provided records of swarms which were fully gregariform (Pasquier *et al.* 1979) at roughly comparable times of year in southwestern Arabia – from Dhala on the Yemen/Aden border in August 1949 (Rainey 1962), and from Najran on the Yemen/Saudi border in October–November 1967 (Hadramy, unpublished; FAO, unpublished; Hemming *et al.*, this symposium, fig 5) in both cases probably produced in an area of high frequency summer swarm-breeding in the interior (Popov & Zeller 1963). Conversely, gregariform locusts at low density and solitariform locusts in swarms have both been repeatedly recorded during plague periods. Thus in our view the claim (Hemming *et al.*, this symposium, § 5) that the gregarious populations found during recession periods differ qualitatively from those found during plagues, is inconsistent both with the evidence just illustrated from recession periods, and also with the ranges both of behaviour and of morphometrics shown by gregarious populations in plague periods. Furthermore, although plagues and recessions can usually be recognized, in general terms, as periods of respectively higher and lower population level, no regular, discrete and useful dividing line between 'plague' and 'recession' has yet been found (Rainey 1971), and no qualitative change to mark a 'state of plague' and justify a change in basic strategy.

It has further been suggested (Roffey *et al.*, this symposium) that the bands and swarms found during recessions may be trivial numerically in comparison with the widespread low-density populations within which they are often found. We consider that this view takes insufficient account of the difficulties involved and the resources needed in satisfactory assessments of locust numbers (Rainey, Betts & Lumley, this symposium, § 2), and of the resulting limitations of such data as have been cited for quantitative evidence to this effect, for example in Roffey, Popov & Hemming (1970). In this latter paper, moreover, no mention is made of the evidence of possible gregarious antecedents for all three of the large low-density populations cited (W13, W16, and Tamesna June 1967) which is on record to suggest possibilities of temporary dissociation. This view of Roffey *et al.* also appears to suggest that the Desert Locust populations at low and high densities, between which it postulates qualitative differences, are likely to remain distinct even within the same environment, despite direct field evidence to the contrary demonstrating the speed and completeness with which effects of the immediate environment (physical or social) can apparently swamp possible effects of the antecedents of the locusts concerned (Rainey 1962; Roffey *et al.* 1970). We consider the appearance of Desert Locusts at low density as commonly only a temporary occurrence in the lifetime of the individuals concerned, and not as a manifestation of any significant separate series of populations at normally low densities.

We fully agree that the swarms found during recession periods are characteristically small, and probably never attain the sizes of the order of hundreds of km^2 which often occur during plague periods, though still likely to outnumber substantially contemporary locusts at low densities. The greater mobility of larger and higher flying swarms ($> 10\ km^2$; Rainey 1958, 1963*b*), recently further established by Draper (1979) may well help to account for the greater extent of the invasion area relative to the recession area (Waloff 1966), as an alternative or supplement to the earlier explanation attributing this difference to low night temperatures limiting the distribution of night-flying low-density populations (Waloff 1962).

(*d*) *Gregarization in context*

Essentially, then, the two hypotheses are, on the one hand, that the kind of continuity which figure 2 suggests so strongly is indeed real and important, as we contend, or alternatively that new major upsurges of the Desert Locust plague start instead with concentration, then increase in numbers and subsequent gregarization of populations living initially (and usually) at very low densities (Hemming *et al.*, this symposium). Figure 2 includes what has very recently been presented (Uvarov 1977) as a particularly well-documented example of this latter process: the build-up in the Tamesna region of Mali and Niger in September–October 1967, observed and described in detail by Roffey & Popov (1968) and already mentioned in this symposium by O.M.S. Abdallahi (§ 2*a*). However, as the diagram and table (W19) indicate, there had been extensive Desert Locust infestations only a few months previously and some 800 km away in northwest Ahaggar, over an area of some 50000 km^2 around Arak, with hopper densities fully comparable with those attained in typical gregarious populations, and against which energetic control operations by the Algerian authorities, from ground and air, had admittedly been incomplete. Although relatively low densities and a lack of gregarious behaviour were initially recorded in the Tamesna observations in September 1967, it is suggested that these are likely to have been temporary effects such as regularly occur even at the height of a plague period. The probability of a link between these locust developments in Ahaggar and in Tamesna was indeed indicated subsequently by Roffey (1969), and is now understood to be accepted (Hemming *et al.* § 3*a*), although not mentioned in an extended account of the 1967 Tamesna gregarization very recently cited in Uvarov (1977).

The evidence available on the possible antecedents of other Desert Locust populations recorded as gregarizing has likewise received but slight attention: every one of the 26 earlier records of Desert Locust gregarization observed or deduced up to 1964 (Waloff 1966) includes circumstantial evidence of a possible connection with earlier gregarious populations – indeed 5 of the 26 cases were during recognized plague periods. For 18 of the remaining 21 cases, during recessions, Waloff records known gregarious populations close enough in time and space to provide potential parents or grandparents, despite the inevitably fragmentary nature of the evidence available; and similarly close gregarious antecedents have since been suggested for two of the remaining three cases (Rainey 1972*a*). The last of these cases of inferred gregarization considered by Waloff (1966) was inadvertently and regrettably overlooked in Rainey

(1972*a*). This was in the Algerian Sahara in May–June 1939 (D. Buxton, personal communication; Pasquier 1942; Volkonsky & Volkonsky 1939), and was assessed by Waloff as F_3 or F_6 to the nearest potential gregarious-progenitors. In this assessment, however, the swarms which had been reported in Niger in 1938 and early 1939, and which had been recorded by B. Zolotarevsky (personal communication) as Desert Locusts, were disregarded, on the grounds (Waloff 1966) of possible confusion with swarms of *Anacridium* which had been present in the neighbouring countries of Mali and the Sudan in 1938, and in Nigeria in 1939. This somewhat doubtful case appears to have represented the nearest approach available, up to 1966, to observed gregarization *de novo* in *Schistocerca gregaria*. Thus most, and possibly all, records of gregarization of this species may well have followed temporary dissociation within the lifetime of the individuals in the population concerned. Even during plague periods, Desert Locusts frequently although temporarily occur at low densities, over areas sometimes of millions of square kilometres (e.g. Sudan/Chad to northwest Africa, September–October 1956). Similarly, during recession periods, the occurrence of locusts at low densities over extensive areas, sometimes of tens of thousands of square kilometres appears to be a characteristically temporary effect: perhaps necessarily so by reason of an inherent instability in such a population distribution (Rainey 1965). Thus if an extensive low-density population encounters the rains which are essential for its successful breeding, the convergent wind-fields necessarily involved in the meteorological mechanism of these rains, successively on synoptic and mesoscales, must be expected to concentrate airborne locusts, probably ultimately to within range of mutual perception (Rainey 1976), when the beginnings of gregarious behaviour may be expected. If such rains are not encountered, the population has no future.

With this species – outstanding in its gregariaptitude (Ellis 1972), rather than in phase lability as Hemming *et al.* (this symposium) envisage – gregarization has indeed been found to occur with such readiness, speed and frequency – during plague periods as well as during recessions – that observations of gregarization have rarely if ever been found of any value in the forecasting of major upsurges, in collective forecasting experience extending over three decades. None of the earlier cases of gregarization appear in fact to have played any major part in the overall development of the plague, since substantial gregarious populations were already present elsewhere in each of these cases; and gregarization has often occurred without upsurge. Personal observation of various stages of gregarization (in Eritrea, Sudan and Saudi Arabia in 1950), at the same time as attempting to assess the changing Desert Locust situation throughout eastern Africa and Arabia and to forecast its development, provided one of us (R. C. R.) with an early lesson in the particular importance of considering such observations of gregarization in the context of the current locust situation, in neighbouring areas and elsewhere, in order to avoid over-estimating their overall significance (Desert Locust Survey 1953).

But it must be emphasized that none of the links suggested in our diagram has been *proved*; in no case have we had an opportunity to study the available evidence, on the locusts and on their environment, as comprehensively as was done, for example, in the case-studies sponsored by W.M.O. on the 1954–5 plague situation (Rainey & Aspliden 1963), and one of the main reasons for originally preparing figure 1 for publication was indeed as a framework for coordinated case studies in the countries concerned.

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(*e*) *Forecasting from the hypotheses*

With the characteristically incomplete and fragmentary evidence so far available, the choice between the two hypotheses remains a matter of opinion. However, the ultimate test of any hypothesis is of course its predictive value. It so happens that there is on record another 'natural experiment', on this point: unplanned but of direct relevance. Over the whole period from before the start of the recession in the early 1960s until 1973, a centralized Desert Locust Information Service (D.L.I.S.) providing regular forecasts and warnings, for all countries invaded or threatened by the species, was operated under the sponsorship of FAO; and the operation of the service was regularly monitored, critically and usefully, by FAO committees representing the national and regional locust control organizations concerned. Until 1967 these forecasts (Betts 1971, 1976) were based on our continuity hypothesis; after that date, as an almost fortuitous result of a reorganization of the service, the alternative older hypothesis, attaching greater importance to the build-up and gregarization of previously solitary-living populations, became the basis of forecasting, and remained so until 1973. Each hypothesis thus had a clear run of 6 years or so to test its value and limitations as a basis for forecasts and warnings, mainly under recession conditions but also including occurrences of upsurge in both cases, and the corresponding published committee reports (FAO 1966, 1972) provide evidence of a marked difference between these two periods in the value of the service to the countries concerned. As is usual with natural experiments, the design was not perfect; there was for example no replication; and, more important, no more detailed assessment has yet been made of this evidence on the relative forecasting performance of the two hypotheses. We would suggest such an assessment as an essential part of placing on record the experience of the past for the guidance of those responsible for Desert Locust forecasting in the future.

3. The African armyworm

When we first became involved with the African armyworm, 12 years ago, we naturally began by applying to it the kind of biogeographical approach which had been developed for work on the Desert Locust. This involved systematically mapping the detailed distribution of all recorded infestations or other occurrences of the species, and following in detail the changes in this distribution with time (Brown, Betts & Rainey 1969). For each recorded infestation of armyworm larvae, we followed our standard Desert Locust practice (see, for example, Rainey & Aspliden 1963) of integrating this into the information available independently on the adults, by estimating, as accurately as possible, when the eggs which produced the larvae were likely to have been laid, and when any moths developing from them could be expected to have emerged. For a large proportion of the infestations of larvae we found that there were, as with the Desert Locust, records of earlier infestations at appropriate times and places to have provided potential parent populations (see, for example, figs 6 and 17 in Brown *et al.* 1969, fig. 6.7 in Betts 1976), if account is taken of what is known of the flight performance of the moths – found to fly up to 24 h at a stretch on a flight-mill (Aidley 1974) – and with recent circumstantial evidence even suggesting 2000 km flights from Australia to New Zealand (Fox 1971, 1973). Of the past 17 years of relatively homogeneous records in eastern Africa, all ten of the years of heavier attacks showed continuous periods of sequences of infestations, lasting up to 9 months with successions of up to seven generations (the armyworm season, Odiyo, this symposium, § 3); during each of

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the seven seasons of lighter attacks, the record showed gaps equivalent to one or two generations. The connections so inferred between successive infestations imply flights commonly over distances of 100–500 km and ocasionally longer.

It was however very clear that reporting was incomplete on many and probably most occasions, and geographical coverage was heavily weighted by the distribution of crops and indeed of human population; nevertheless, and again as with the Desert Locust, it repeatedly seemed that what had been reported provided circumstantial evidence about what had been missed, especially in relation to timing. Thus a few reports of small-scale infestations could often be suggested, with benefit of hindsight, as evidence of more extensive infestations at a similar stage of development in surrounding areas.

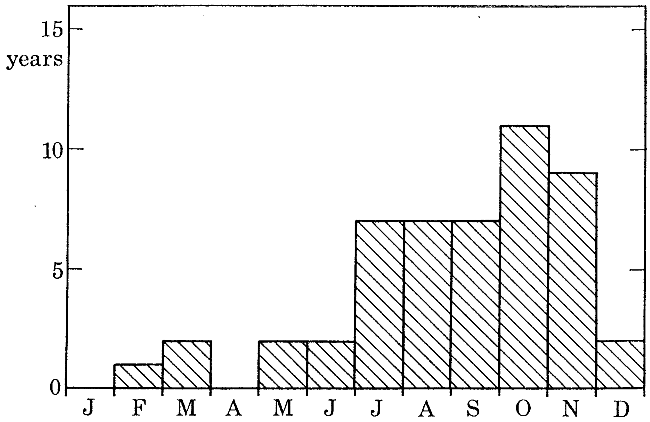

FIGURE 3. Strategy of armyworm control in Africa: the basic question. Number of years *without* reports of infestations of *Spodoptera exempta* larvae anywhere in Africa in a particular month during the 16 years 1961–76 (compiled by M. J. Haggis). The species has a life cycle of 4–6 weeks, and has so far appeared to be virtually without a resting-stage.

Again as with the Desert Locust, this approach has not only suggested these possible links, but has directed attention to potentially significant gaps in the story, when no such link can be suggested. For the African armyworm, there is in almost every year a period of several months between 'armyworm seasons' when contact appears to have been lost with the main populations of the species (figure 3); and one of the most important results of this approach has in our view been that of formulating the question where and in what form are most of the individuals of this species to be found during October and November – either hidden (Rose, this symposium, § 2), by reason of passive behaviour, low density and/or diapause – or unrecorded, somewhere in grasslands or savanna without cultivation and perhaps without inhabitants.

4. Some implications

Most records of high-density populations both of the Desert Locust and of the African armyworm are suggested as representing intermittent contacts with varying proportions of a few series of mobile regional populations, with each of these reports accordingly helping to provide warning of when and where the next might be expected. Moreover, control operations against each generation might well therefore reduce the possible scale of operations needed against the next generation, in a potentially cumulative mannner which could not be expected if these attacks were due to separate and independent populations. This particular question of alternative hypotheses is indeed no mere matter of semantics or of academic hair-splitting, but a question of crucial importance in the development of improved strategies of control for both species.

It can now be claimed that some of the key questions have been formulated for the improved control of both these major pests; and furthermore new methods of field research, using aircraft and radar (Schaefer, this symposium), have now been developed elsewhere to answer just such questions. Airborne insects can now be systematically sought, in relation to the wind systems in which they fly, and their distribution, behaviour and displacements can now be investigated, just as envisaged 10 years ago by Vernon Joyce (1968), in places and at times (particularly by night) when such phenomena are otherwise largely inaccessible for study. In this way it now appears technically possible that the gaps in space and time when contact is currently lost with the major populations of these pests (whatever their density) could be narrowed down very considerably, in a manner suggested retrospectively (Rainey 1973, fig. 10) for e.g. the Desert Locust situation of June–October 1967 in northeast Africa, a time of year and an area in which radar and an appropriately instrumented aircraft were immediately successful in locating and sampling high-flying grasshoppers (*Aiolopus* and *Catantops*) in the intertropical convergence zone (Rainey & Joyce 1972; Schaefer 1976). (A similar retrospective suggestion has since been made for searching the Zaire air boundary over Zambia and neighbouring countries for the critical initial armyworm moth population on October 1971; Rainey 1979). Meanwhile, differences in opinion on the behaviour and distribution of the insects during these gaps remain inevitable and even desirable.

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Appendix. Main Desert Locust populations reported

(July 1963 – September 1967)

Area west of 25° E

serial number	*month and year*	*country and locality*	*locust population*
W1	April–May 1964	*Chad* – near Bardai in Tibesti	adult locusts seen in grass by méhariste
	May 1964	*Chad* – near Bardai in Tibesti	thin flight or swarm ('vol diffus') seen by méhariste
W2	May–June 1964	*Algeria* – S. Ahaggar, 40 km S of Silet	scattered hoppers over tens of hectares, noted by local people
	June 1964	*Algeria* – Silet	young adults, largely or perhaps wholly isolated, seen flying over Silet
	June 1964	*Algeria* – Amdad (25 km NNW of Silet)	young adults seen settled for several days
W3	June 1964	*Algeria* – Aoulef	several reports of a light flight or swarm ('? léger vol'), individually unconfirmed
W4	June 1964	*Libya* – 50 km SW of Hon	20 bands IV+V instar hoppers; fledglings: control over 6 ha, 9 l 30 % aldrin and 175 kg bran mixed 8 % with 20 % BHC
W5	July–October 1964	*Chad* – Ennedi	scattered locusts; in Sept. at densities of 1/100 paces over distances of 80 and 100 km with concentrations of locusts up to 20/100 paces
W6	December 1964 January 1965	*Algeria* – Tindouf *Mauritania* – Fort Trinquet	small scattered swarms of unidentified species, probably *Schistocerca*
W7	May–June 1965	*Morocco* – SW Anti-Atlas (Mader Anzis, Foum el Hassan, Assa, and Akka)	hopper bands over 2 km² confirmed by presence of droppings and moult skins, and 4 reports of small swarms
W8	July 1965	*Mauritania* – between Atar and Fort Gouraud	thin swarm of unidentified species reported by aircraft at 1000 m.
W9	September 1965	*Mauritania* – near Nouakchott	control against dark pink solitariform scattered locusts; densities low over 300 km², up to 20/100 paces over 100 ha: 1300 litres 5 % dieldrin used
W10	October 1965	*Niger* – Tamesna and western Aïr	locusts scattered at low densities at intervals over at least 50000 km²: in one area of 1 km², 5 egg pods/m² (maximum 16), 1 hopper/m²
W11	October 1965	*Chad* – Djourab	1–5 locusts per hectare over 5000 km²
W12	November 1965–January 1966	*Algeria* – Tassili des Ajjers around Djanet	17 adults and 53 larvae captured during November, 90 adults and 166 larvae captured during January and numerous adults seen
W13	December 1965	*Mauritania* – near Atar	scattered locusts and hoppers of all stages over 20000 km², densities 1/100 paces, locally up to 30 per hectare
W14	February–March 1966	*Mauritania* – Fort Gouraud, Oued Oum Dheferat	control of scattered adult locusts at 50–100 locusts/100 paces over 400 ha; 500 l 5 % dieldrin used
W15	June 1966	*Niger* – Ouallaram	several reports of swarms of 'numerous locusts' on two occasions some 10 days' apart: specimens of solitaricolor *Schistocerca* collected by villagers and sent to local locust scout; several local cultivators subsequently selected a specimen of *Schistocerca gregaria* rather than *Anacridium melanorhodon* and *Ornithacris turbida* (both present locally) as the species concerned
W16	August–September 1966	*Chad* – Tibesti	control of hoppers and fledglings at 30–100/100 paces over 110 km²; 2000 l 5 % dieldrin
W17	November 1966	*Mali* – Tilemsi Valley	control of hoppers (10/tuft) and fledglings (80/100 paces) over 2 km²; 1200 l 5 % dieldrin

Serial number	*Month and year*	*country and locality*	*Locust population*
W18	November 1966	*Libya* – Fezzan, SW of Uau el Khabir	control against V instar hoppers and fledglings in an area approx. 60 km^2; 40 kg aldrin 24 % in a 2 % spray and 300 kg 8 % BHC
W19	March–June 1967	*Algeria* – NW Ahaggar, within total area of about 250 × 200 km around Arak	adults up to several thousand per *Acacia*; hopper densities in May/June up to more than 1000/m^2 at hatching and about 100/m^2 in later instars; 1080 kg $3\frac{1}{2}$ % γBHC dust, 3360 l, 15 % BHC spray, and 5750 kg 0.2 % γBHC bait applied over net infested area of more than 10 km^2
area between 25 and 50° E			
C1	July–October 1963	*Ethiopia/Somali Republic* (*N*) – Dessie/Awash/Borama	2 reports of swarms, with further 5 reports of swarms recorded as unconfirmed; small groups of hoppers found following one of above reports;
		Berbera	scattered pink locusts
C2	March–April 1964	*Ethiopia* – Eritrean coast, Addis Ababa, Ogaden, Danakil	yellow locusts seen in widely separated areas, with unconfirmed report of swarm in Danakil
C3	August–September 1964	*Ethiopia/Somali Republic/* Gulf of Aden	2 reports of red swarms, and 3 further reports of swarms recorded as unconfirmed together with one aircraft sighting of suspected swarm (Rainey 1972*a*), recorded 1533/11 Sept. at 10.15 N 42.20 E, and closely resembling fig. 5.23 in Rainey (1976)
C4	September–October 1964	*Saudi Arabia* – Gizan area	control against scattered hoppers and adults together with *Anacridium* and other grasshoppers
C5	October 1964	*Sudan* – Northern province east of Merowe	hopper bands; hoppers and fledglings at 4 per square metre sprayed with about 200 U.S. gals 20 % dieldrin at 7 fluid oz/per feddan (implying a net infested area of approx. 15 km^2) in 2 areas totalling 45 km^2 gross; similar infestation in a neighbouring area was not sprayed. Unconfirmed report of swarm
C6	November 1964	*Somali Republic* (*S*) Dusa Mareb and neighbouring areas, and inland from Mogadiscio	1 swarm report and 2 others regarded as unconfirmed; scattered locusts found
C7	December 1964–February 1965	*Ethiopian coastal area*	swarm ($1\frac{1}{2}$ square miles), estimated to contain some 3 million locusts: hopper bands; control (3 bags 10 % BHC) over 60 square miles
C8	January 1965	*Somali Republic* (*S*) Balad, Busar and Bardera	3 reports of swarms, individually unconfirmed
C9	January 1965	*Ethiopia* – Urso	unconfirmed report of swarm, followed by unconfirmed report of scattered locusts near Harar in February
	January 1965	*Somali Republic* (*N*) Sillil	locusts in 4s and 5s over some 1370 square miles
C10	January–March 1965	*Saudi Arabia* – S. Tihama	control against 8500 II–V instar hopper bands, seen at intervals over a distance of 200 kms and in one locality marching distances of kilometres; 4 tons 20 % BHC, 7 tons poison bait used (Mohamed & El Khatim 1965)
	March 1965	*Yemen* – Tihama 400 km S of above	control against 200 small bands hoppers scattered over about 30 km^2, 10–50 hoppers per bush, mixed with larger numbers of *Anacridium*; 100 kg BHC, 1 ton bran, 300 kg rock phosphate used

Serial number	*Month and year*	*country and locality*	*Locust population*
C11	May–June 1965	*South Arabia* – 75 km NE of Aden	pink swarm (2 square miles)
		within 25 km of above	scattered pink locusts at 2 places
		Aden	isolated locusts
		Upper Yafaa, 115 km NE of Aden	locusts on sale in Aden market about one month later than first swarm report and said to have come from Upper Yafaa
C12	May–July 1965	*Ethiopia* – Awash/ Afdem area	unconfirmed reports of swarms in 5 localities within a distance of 125 kms, including 3 independent reports of a swarm in one of these localities; no locusts found during ground surveys
C13	October 1965	*Somali Republic* Garoe area	locusts seen in hundreds or thousands, initially reported as a swarm
		Hiran province	2 unconfirmed reports of swarms
		Central Mudugh	unconfirmed report of scattered locusts
C14	January 1966	*Somali Republic* – Abduuch, Mudugh province	swarm reported and scattered gregariform locusts found 7 days later
C15	January 1966	*Ethiopia* – Wadi Teclai near Sudan border	laying swarm, found to be $\frac{1}{4}$ square mile by locust officer 7 days after arrival; density up to 24 locusts/m^2
	February–March 1966	*Ethiopia* – Wadi Teclai near Sudan border	control against 517 hopper bands totalling some 20 hectares, using 400 kg BHC dust; fledgling April
	February–April 1966	*Sudan* – S coastal area adjoining above	control of groups and marching bands of hoppers in areas totalling some 140 km^2, 73 gals dieldrin used during first month of operations
	February 1966	*Ethiopia* – Takazze valley headwaters	Scattered locust hit by aircraft and others seen
C16	June 1966	*Somali Republic* (*N*) Las Anod area	scattered locusts flushed over a distance of 40 miles (65 km), maximum density 11/100 yards. Scattered locusts had appeared over an area of at least 2600 km^2
C17	October–December	*Somali Republic* *Ethiopia*	unconfirmed reports – swarms (2 reports), hopper bands (1) Groups of locusts (1) and scattered locusts (1)
C18	March 1967	*Jordan* – Hassa	unconfirmed report of yellow swarm at date approximating to inferred laying date U.A.R./ Sudan border (see below)
C19	May 1967	*U.A.R./Sudan border* – coastal area	control against late-instar hoppers in very dense patches (4 m^2, density 500 m^{-2}) over 375 km^2; scattered fledglings over 1500 km^2. 500 kg 20 % BHC dust and 3000 kg bran used
area east of 50° E			
E1	July 1963	*India* – Jaisalmer	2 reports swarms, both approx, 4 km^2
		Pakistan	
	July 1963	Khairpur	swarm, 1 mile radius
	August 1963	Mirpur Mathelo	unconfirmed report, group of locusts
	September 1963	Multan	unconfirmed report of swarm
E2	December 1963	*Pakistan*	
		Mirpur Khas	unconfirmed reports of swarms from 3 villages; report of locust concentration $\frac{1}{4} \times \frac{1}{8}$ miles
	December 1963	*Pakistan* – Larkana	unconfirmed report of swarm, $\frac{1}{2}$ square mile
E3	April 1964	*Oman* – Abu Dhabi and Buraimi	2 unconfirmed swarm reports
		Dhaid	scattered locusts confirmed

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Serial number	*month and year*	*country and locality*	*Locust population*
E4	April–May 1964	*Pakistan* – Turbat	control against hoppers at a density of 1000/acre in 10 square miles; 224 lbs 1% and 12% BHC used: Pinkish-yellow adults
E5	June 1964	*Iran* – Jiroft	IV and V-instar hoppers seen in an area of 50 hectares; 2 small swarms adult locusts, 4000–5000 m² and 500 × 200 m mixed Desert Locusts (40%) and 'native locusts' (60%); control, 12% BHC and bran
E6	June–November 1964	*India* and *Pakistan*	73 separate reports of swarms and bands: control in both countries; 15,605 kg 10% BHC dust and 3258 l 20% and 40% dieldrin and aldrin applied over 82 km² in India
E7	March–May 1965	*Pakistan* – Kulanch and and Dasht valleys	control against groups and isolated hoppers and adults and 'gregarious breeding'; 680 l 20% dieldrin and 2 tons 12% BHC applied over about 900 km²
	May 1965	*Pakistan* – Ferozabad (Khuzdar district)	groups of about 80 locusts scattered over 8 square miles
	June 1965	*Pakistan* – Pasni	unconfirmed reports of swarmlets
E8	July 1965	*Pakistan* – Bahawalpur	unconfirmed report scattered hopper populations in ½ square mile
	August 1965	*Pakistan* – Bahawalpur	unconfirmed reports swarm and 'high' scattered locust populations
	August–September 1965	*India* – Rajasthan (Bikaner, Jaisalmer and Jodhpur districts)	control of scattered *Schistocerca* hoppers together with *Oedaleus* over 290 hectares (9777 kgs 10% BHC and 79 litres 20% dieldrin)
E9	December 1965	*Pakistan* – Panjgur	report of swarm by revenue officer; droppings found by central government locust officer, but no specimens with wings could be found; size – ½ acre swarmlet
E10	March 1966	*Trucial Oman* – 30 km E of Sharjah	first-instar hoppers initially reported as 2–5 per bush over 100 km²; subsequently control by exhaust sprayer over 15 square miles where the vegetation cover was good and the population most dense; 30 gals dieldrin used
E11	March 1966	*Pakistan* – Dalbandin (Chagai district)	copulating adults in 4 square miles controlled by BHC dusting
	May 1966	*Pakistan* – Chagai district	first-instar hoppers controlled in 1 acre
E12	May 1967	*Muscat* and *Oman* – Salalah	groups and isolated recently-fledged *Schistocerca* and other acridids flying nightly round meteorological station for at least 11 nights

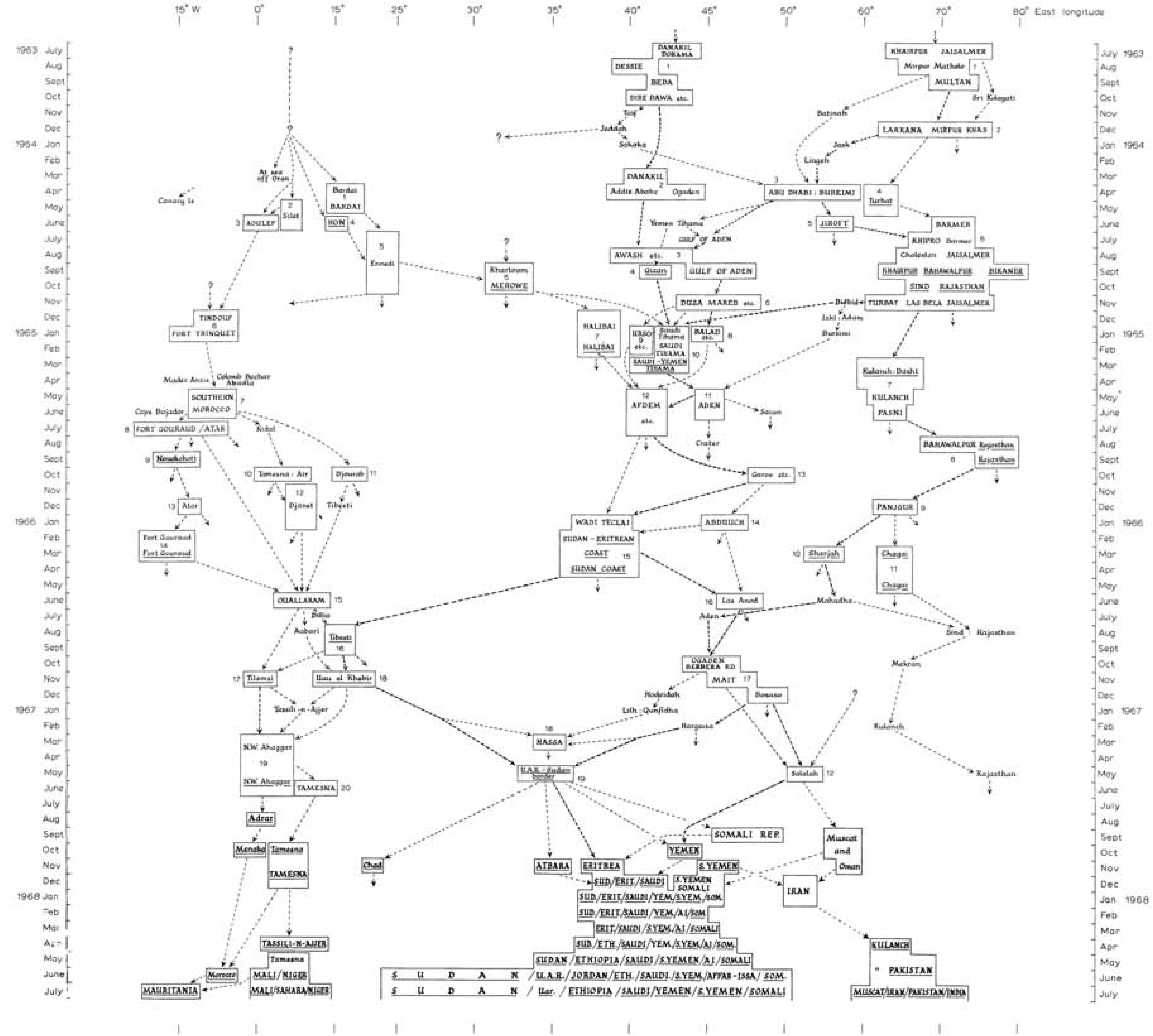

FIGURE 2. Desert Locust recession and upsurge 1963–8: a preliminary outline. Main reported locust populations indicated by framed locality names in appropriate month(s) and at approximate longitudes, numbered to correspond with lists in the appendix and underlined if control measures undertaken; reports of gregarious populations (swarms of adults or bands of nymphs) in CAPITALS, those of locusts not in swarms or bands in lower case. Limited selection of other locust reports shown by unframed locality names, e.g. Hargeisa.

The original list and diagram included reports up to May 1967, and were completed in September 1967, very shortly before the upsurge became apparent. The diagram was later extended to July 1968, to cover the upsurge, but no amendments were made – or needed – in the continuing links which had been inferred earlier.