

Windborne displacements of Desert Locusts from Africa to the Caribbean and South America

Jane Rosenberg* & Peter J.A. Burt

Natural Resources Institute, University of Greenwich, Central Avenue, Chatham Maritime, Kent ME4 4TB, UK
(*author for correspondence, e-mail: l.j.rosenberg@greenwich.ac.uk; fax: +44 1634 883232)

Received 1 October 1998; accepted in final form 25 March 1999

Key words: Atlantic Ocean, flight-duration, Locust, long-distance migration, *Schistocerca gregaria*, trajectory analysis

Abstract

The Desert Locust is a major pest of agriculture in Africa, the Middle East and South-West Asia and swarms are known to make downwind flights over hundreds and thousands of kilometres between seasonal breeding areas. At the end of summer in 1988, swarms of locusts were moving north and south along the western margins of North Africa and in October and November, swarms crossed the Atlantic Ocean and invaded the Caribbean and neighbouring parts of South America for the first recorded time. Because of the extent of the migration and the evolutionary significance of linkages between Old and New World species of locusts, the weather associated with the migrations was studied and trajectory analysis was used to identify the source areas and estimate the flight times. Locusts were moving offshore from western North Africa throughout the autumn and on three occasions migrated west of 40° W with easterly Trade winds. Two trans-Atlantic crossings coincided with the passage of easterly waves. Over 100 trajectories were constructed at 950 and 850 hPa and within the time limit used (≤ 144 -h), 28% successfully linked source and receptor areas. Minimum trajectory duration was 93-h, which is one-and-a-half times longer than the previously longest flight duration, derived for a similar migration to the British Isles in 1954. Upwind trajectories from the arrival areas, identified sources between 27 and 6° N in Africa, with most end-points located in Mauritania, Senegal, Gambia and Guinea-Bissau. Interspersed with the Atlantic crossings were a northward movement of locusts and an incursion of Saharan dust into Europe within the circulations of frontal depressions. While offshore migrations from northern Africa are common in autumn, the immigrants in the Caribbean and South America were probably at the extreme limits of flight endurance for the species. The results tend to confirm earlier hypotheses that New World species of locusts may have evolved from ancestral migrants from Africa.

1. Introduction

Plagues of the Desert Locust, *Schistocerca gregaria* (Forskål) can spread intermittently over 20% of the Earth's surface, covering 65 countries in Africa, the Middle East and South-West Asia (Figure 1). The species has no permanent breeding area, but lives in a generally arid environment from Mauritania to north-west India and a key factor in its survival is its ability to fly hundreds or even thousands of kilometres between seasonal rainfall areas in order to breed (Figure 1). The association between the

migration of locusts and the prevailing winds has been recorded since biblical times (e.g., Exodus, Chapter 10) and understanding and recognising the main seasonal migration and breeding patterns is an important part of forecasting changes in the size and distribution of populations.

In 1985, the first Desert Locust plague for 16 years began near the Red Sea and over the next three years good seasonal rainfall throughout the locusts' distribution area ensured that populations built up. By the end of summer in 1988 swarms (cohesive units containing tens to hundreds of millions of adults per

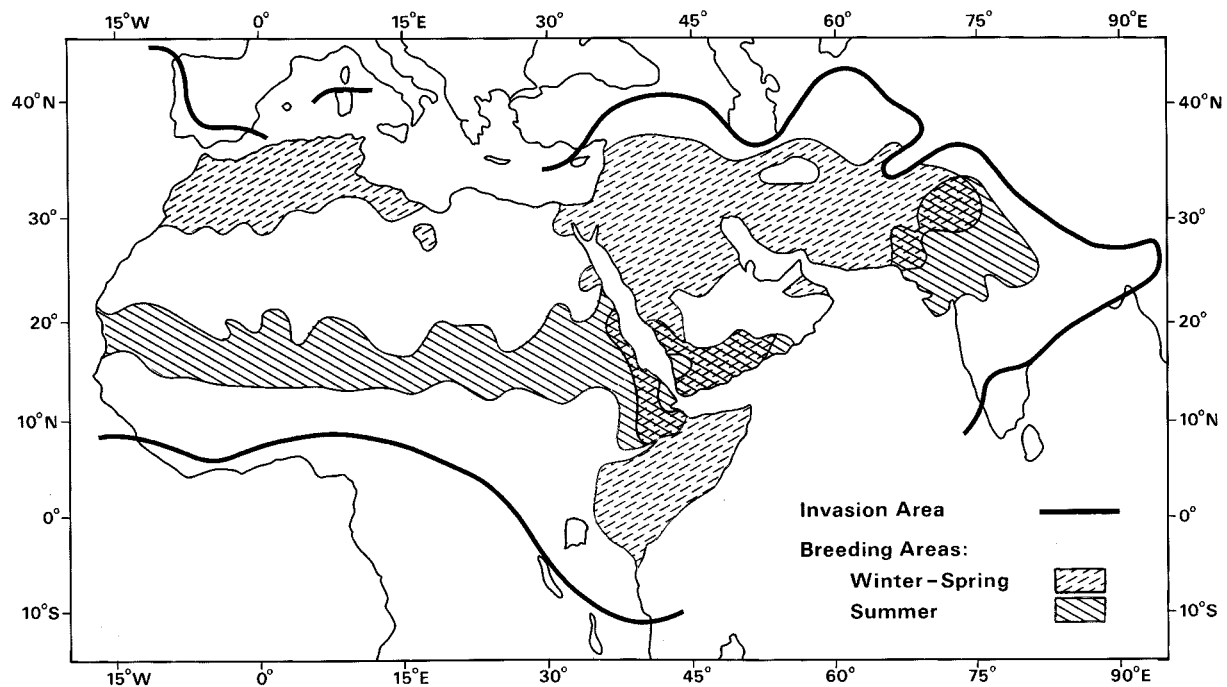


Figure 1. Main seasonal breeding areas of the Desert Locust and limits of swarm invasions during plagues (after Waloff, 1966).

square kilometre (Pedgley, 1981)) were reported right across the Sahel and beginning to move northwards towards the winter/spring breeding areas of north-western Africa. Between 9 October and 8 November, Desert Locust swarms invaded the Caribbean and adjacent parts of South America after a sea crossing of some 5000 km (Figure 2). While the immigrants were subsequently of no economic significance, this unique event is important to understanding both the processes of insect migration and the evolutionary significance of linkages between Old and New World species of locusts (Ritchie and Pedgley, 1989; Richardson and Nemeth, 1991). In this paper, trajectory analysis, which has been used to study the oceanic transport of airborne dust (e.g., Coude-Gaussen et al., 1987; Bergametti et al., 1989; Whittlestone et al., 1992; Ellis and Merrill, 1995), is used for the first time to identify the sources of the Desert Locusts which invaded the Caribbean and South America in October and November and to estimate the duration of the migratory flights.

2. Materials and methods

2.1. Locust migratory flight behaviour

Unlike other airborne particulates, insects are not passively transported “aeroplankton”, but actively direct their flight upwards at take-off, maintain flight by flapping and gliding once airborne and end their migration by ceasing wing flapping (Pedgley, 1982). Trajectories can be used to depict the tracks of migrating insects when temperatures do not inhibit flight and wind speeds exceed the insects’ airspeeds, so that the direction of migration is determined by that of the wind and its extent is a function of wind speed and the insects’ intrinsic flight capabilities (Rosenberg and Magor, 1983). Since wind speed and direction vary with time and altitude, the times of take-off and the duration and height of flight must be assessed before windborne movements can be modelled. Values for these flight characteristics, derived from previous field and laboratory observations (e.g., Kennedy, 1951; Sayer, 1956; Weis-Fogh, 1956, 1976; Rainey, 1963; Johnson, 1969; Waloff, 1972; Pedgley, 1981) suggest that swarm migration begins a few hours after sunrise once the locust’s flight muscles are warm enough to sustain wing beating. Once airborne, swarm displacement is downwind and is limited by temperature to the lowest

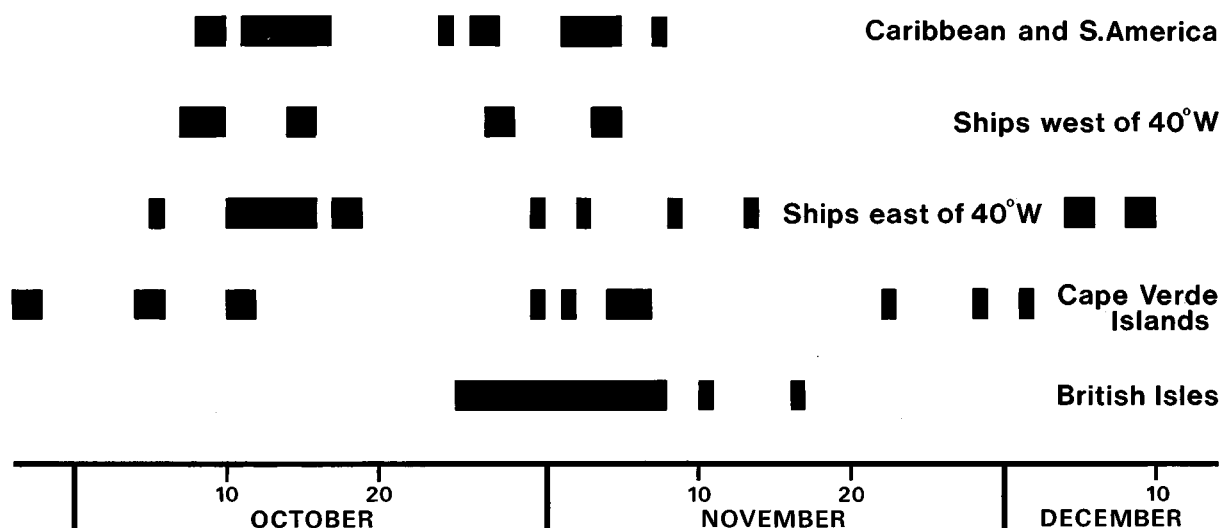


Figure 2. Dates of reports of Desert Locusts (■) on the Atlantic Ocean and in Europe, the Caribbean and South America, September to December 1988.

2 km of the atmosphere (the approximate temperature threshold is 20 °C). Within a swarm, locusts do not have any single preferred orientation and turn back towards the centre when they reach the edges in order to maintain swarm cohesion. Thus, although locusts' air speeds range from about 2.5 to 6.5 m s⁻¹, the speed of swarm displacement tends to be the same as the wind speed at the height of flight. Adult locusts are large insects, weighing between 1 and 3 g with a wing span of 10 to 15 cm and without flapping their wings or gliding, would fall to the ground at about 0.3 to 2 m s⁻¹. The ability to sustain flight necessary for long-distance dispersal varies considerably among individuals and estimates of maximum flight duration range from 20-h in the laboratory to 60-h for a migration of 2500 km from North-West Africa to the British Isles in 1954 (Rainey, 1963; Taylor, 1979). Since there is no precedent for a single locust flight of 5000 km, a maximum flight duration of 144-h has been used in this study, based on the duration of transport of Saharan air across the Atlantic (Carlson and Prospero, 1972).

2.2. Insect data

Published and unpublished reports of locust sightings on land and at sea from September to December 1988 were collated from the monthly Desert Locust Bulletins issued by the United Nations Food and Agriculture Organisation (FAO), the FAO's Emer-

gency Centre for Locust Operations (ECLO) archive and the proceedings of a regional meeting held in the Caribbean (Stemshorn, 1989). Reports usually contained information on location, stage of life cycle, sexual maturity, behaviour and estimated size/density of the locust populations. The precise times locusts were sighted are rarely known and observations were usually recorded only to the nearest day. The Atlantic Ocean reports were all from commercial vessels operating in standard shipping lanes.

2.3. Weather data and analysis

The trajectories were calculated in 3-h segments using the UK Meteorological Office global numerical weather prediction model (Gadd, 1985; Cullen, 1993). Since the exact height of flight and any changes in height during the migration are unknown, the trajectories were constructed at the constant geopotential surfaces of 950 and 850 hPa, representing the approximate lower and upper limits of the migrating swarms. Trajectories were drawn downwind from putative source areas in North-West and West Africa between 30° and 15° N and upwind from a number of invasion areas in the Caribbean and South America. Since the times of swarm departure and arrival are unknown, all trajectories were started at 1200 GMT. Trajectory construction was stopped at the arbitrary time limit of 144-h and trajectories were halted when they reached land or were within 1° to 2° latitude/longitude (100–

200 km) of land. To examine the effect of the locust's own air speed on trajectory duration and to simulate the displacement of locusts with a constant downwind orientation, some trajectories were constructed with the addition of a flight velocity of 2.5 m s^{-1} , the minimum powered flight recorded (Weis-Fogh, 1976). Radiosonde and pilot balloon data for the study period were also obtained for 3 stations along the western North African coast at Nouadhibou ($20^{\circ}56' \text{ N } 17^{\circ}02' \text{ W}$), Nouakchott ($18^{\circ}06' \text{ N } 19^{\circ}57' \text{ W}$) and Dakar ($14^{\circ}44' \text{ N } 17^{\circ}30' \text{ W}$) and for Santa Cruz in the Canary Islands ($28^{\circ}28' \text{ N } 16^{\circ}15' \text{ W}$).

3. Results

3.1. Source areas and migration sequences

Swarms and groups of immature and mature locusts had invaded western North Africa and North-West Africa from September onwards, and by mid-September breeding was reported. At first, the predominant direction of swarm movement was to the west and then south across Senegal to Gambia and Guinea Bissau (i.e. between about 15° and 10° N (Figures 3 and 4)). Large swarms also moved westwards and northwards along the coast in Mauritania (i.e. north of 15° N (Figures 3 and 4)) and by the end of September, swarms were probably moving north of 20 to 25° N , through northern Mauritania and the western Sahara. The area covered by Desert Locusts in North-West Africa was augmented by massive invasions northwards and north-westwards from the Sahel to Algeria in September and October and to Morocco between October and December.

Analysis of reports from the Atlantic showed that Desert Locusts were moving offshore from Africa over a two month period between the end of September and the beginning of December 1988 (Figure 2). Scattered locusts were first reported from the Cape Verde Islands on 27 to 28 September, followed by a series of reports from ships on the Atlantic between 10 and 20° N and 20 to 60° W and culminating in the first reports of Desert Locusts in the Caribbean from 9 to 17 October (Figure 2). The invasions of the Cape Verde Islands continued intermittently until 2 December and Desert Locusts were reported from ships east of 40° W up to 10 December. West of 40° W , there appear to have been two further incursions by Desert Locusts, from 25 to 29 October and from 2 to 8 November, which affected mainland countries such as Surinam, Guyana

and French Guiana as well as the Caribbean (Figure 2). During the same period, locusts were observed in the south-western parts of the British Isles on 26 October and were subsequently reported more or less continuously until 17 November, although it is unclear whether the November sightings in Britain represented later arrivals or survivors from the October invasion.

3.2. Weather during the migrations

From September to December the weather over the Atlantic was dominated by the Azores-Bermuda anticyclone with the Azores high pressure centre at about $34^{\circ} \text{ N } 37^{\circ} \text{ W}$ and north-east and easterly Trades to the south. The intensity, position and form of the anticyclone varied from day to day during the study period. At times, it intensified and shifted eastwards, leading to an offshore easterly wind flow over western North Africa. As the frequency of frontal depressions increased during the autumn, the high pressure centre weakened and winds over North Africa became easterly or south-easterly as cold fronts approached the coast from the west and north-west. The Inter-tropical Convergence Zone retreated southwards from about 20° N in September to a surface position of 5° N by December, although there were considerable day to day variations in position. Two tropical cyclones affected the western Atlantic Ocean during the invasions of the Caribbean and South America, both developing from easterly waves emerging from western Africa at about 10° N (Richardson and Nemeth, 1991). The first, which developed into tropical storm Joan on 11 October left the coast of Africa on 5 October and persisted around the Caribbean Sea and South American coast as a tropical storm or hurricane until 23 October. This was followed by a tropical depression which affected the north-eastern coast of South America from 20 to 21 October.

There are very few radiosonde or pilot balloon observations for western North Africa, but upper air data show that on most days along the western North African coast, a shallow surface layer of moist maritime air was present, capped at between 400 and 1600 m by a strong temperature inversion with warm, very dry air above. The height of the inversion increased westwards from the coast so that at Santa Cruz in the Canary Islands it ranged between 1100 and 2500 m in height.

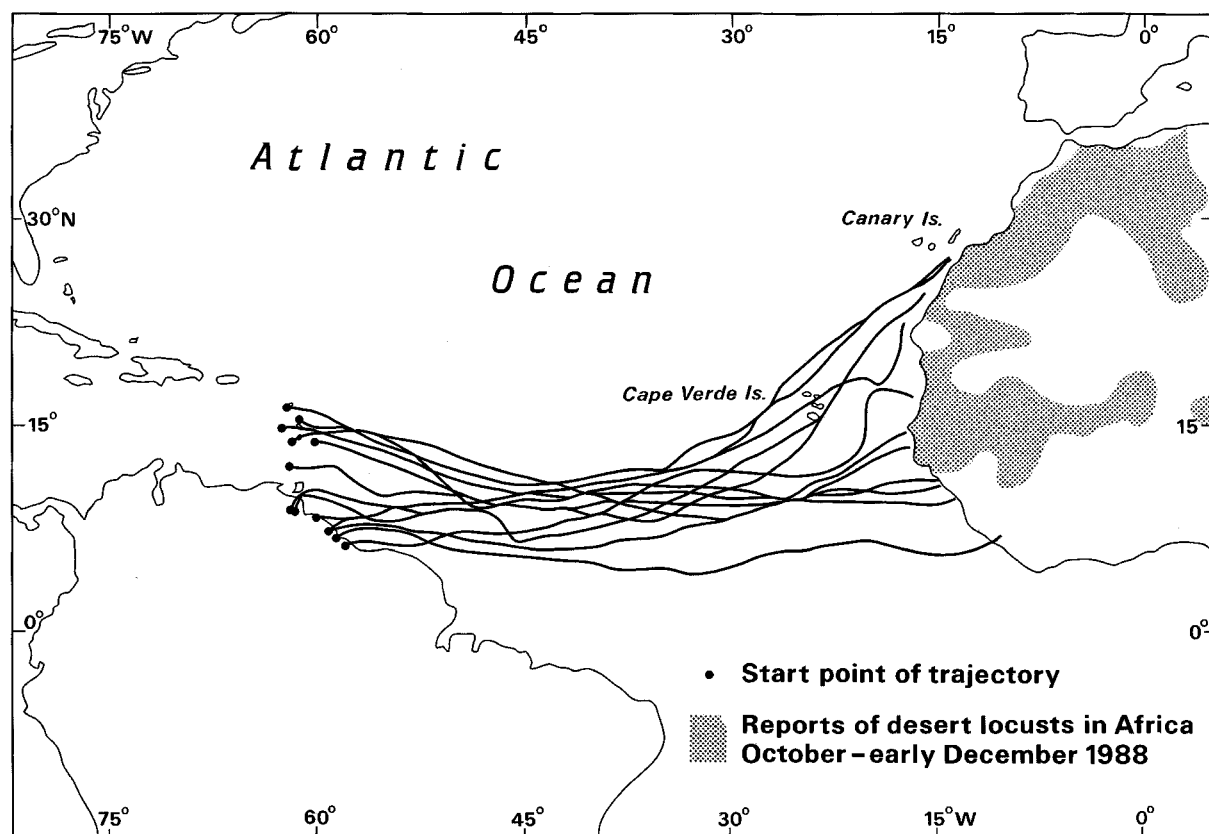


Figure 3. Distribution of Desert Locusts in Africa and 950 and 850 hPa trajectories from the Caribbean and South America during the three invasion periods in 1988.

3.3. Trajectory analysis

A total of 78 trajectories were constructed at 950 and 850 hPa upwind from the Caribbean and South American arrival areas and downwind from putative source areas in Africa. Within the 6 day time limit, only 8 upwind and 10 downwind trajectories linked possible source and arrival areas. Twenty-four trajectories were also calculated with the addition of flight velocity, and of these, 5 upwind and 6 downwind trajectories successfully linked source and arrival areas (Figures 3 and 4). Most trajectories which failed to link possible source and receptor areas within the time limit were constructed in either light and variable winds or rapidly changing windfields associated with the trailing fronts of eastward moving frontal depressions.

Trajectory durations ranged from 96 to 144-h for upwind trajectories and from 93 to 144-h for those constructed downwind. The two shortest durations (93 and 96-h) were associated with trajectories

constructed with the addition of flight velocity, but otherwise the range in durations was similar irrespective of whether flight velocity was added to the calculations. Trajectory durations were also unaffected by the westward passage of the two tropical storms during the first two invasions of the Caribbean and South America.

The trajectories identified the same source areas for all three Caribbean and South American locust invasion periods. Sources were identified between 27 and 6° N in Africa with most end points located between 20 and 10° N in Mauritania, Senegal, Gambia and Guinea-Bissau (Figure 3). Upwind trajectories constructed at 950 hPa tended to locate source areas north of 15° N, whereas 850 hPa trajectories identified sources to the south (Figure 3). Conversely, arrival areas in the Caribbean and South America tended to be identified south of 15° N by 950 hPa trajectories and north of 8° N by those at 850 hPa (Figure 4).

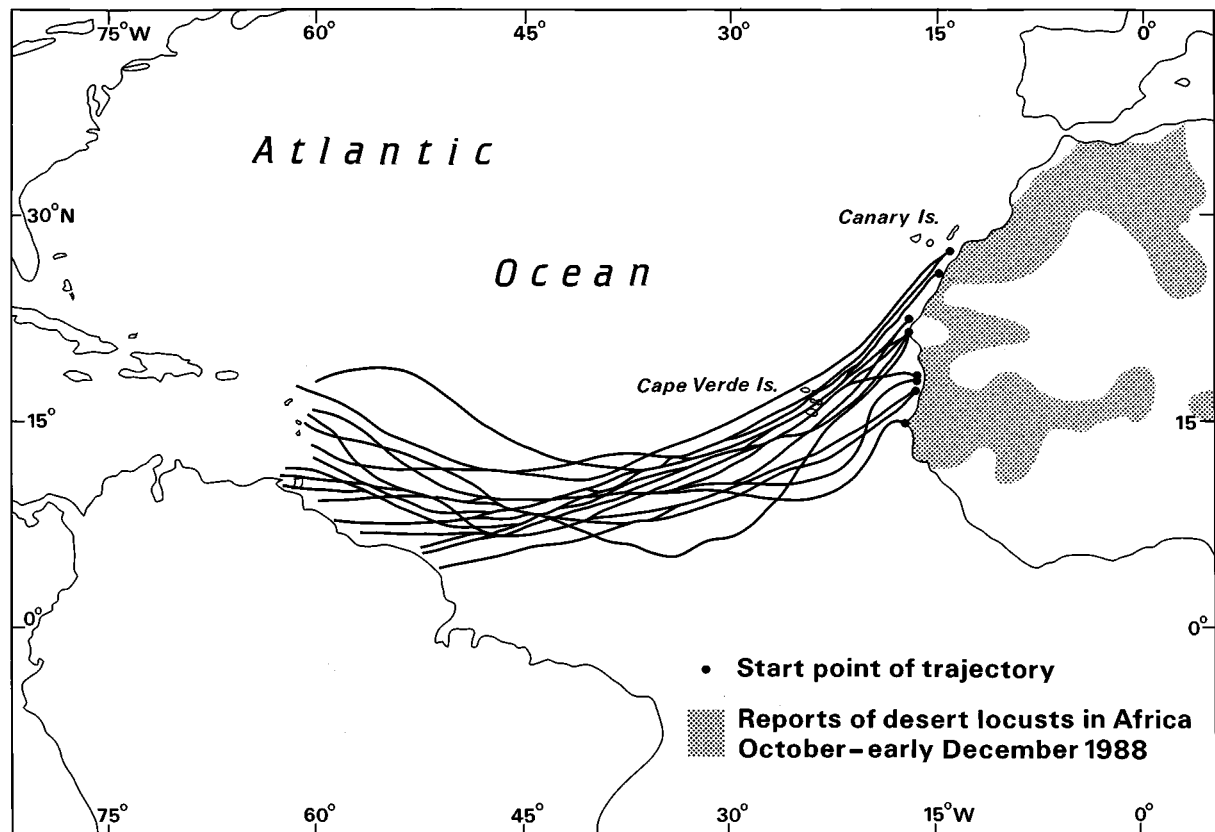


Figure 4. Distribution of Desert Locusts and 950 and 850 hPa trajectories from Africa during the three emigration periods in 1988.

4. Discussion

In this paper, trajectory analysis has been used to locate possible sources and so to estimate the flight duration of Desert Locust swarms that invaded the Caribbean and South America in 1988. Trajectory simulations are most accurate under well-defined, large-scale synoptic patterns such as predominated during this study period, although errors are amplified with increasing time and distance between source and receptor points, particularly when transport time exceeds 24-h (Clarke et al., 1983; Scott and Achtemeier, 1987). The duration of the simulated migrations ranged from 93 to 144 h, but these estimates are subject to three sources of error. First, trajectories were started at 1200 GMT whereas the actual times of swarm take-off and arrival are unknown. Secondly, the trajectories were stopped when they reached land or were within 1 to 2° latitude/longitude of land, although the swarms could have originated further inland and/or continued flying overland in the arrival

areas. Finally, wind-fields constantly change and are affected by small-scale disturbances of a few hours duration and the analysis did not take account of features such as sea breezes which can effect locust movements (Rainey and Waloff, 1948). However, there was no evidence of the presence of sea breezes during the study period from the limited observations available along the coast of western North Africa.

Although the results must be treated with caution, the trajectories do indicate which broad areas were sources for the migrating swarms for all three invasion periods. Most upwind trajectories located sources between Mauritania and Guinea-Bissau (i.e. between 20 and 10° N) and although it is possible that swarms also emigrated from north of 20° N, it's unlikely that locusts originated south of Guinea-Bissau, since swarms were not confirmed south of 10° N until late November. The second and third incursions in the Caribbean and South America in 1988 may have represented redistributions of the earlier arrivals, since the locusts were 'fresher' in appearance (Stemshorn,

1989). However, trajectories linked putative source areas with the Caribbean and South America for all three invasion periods and the sequence of reports in 1988 (Figure 2) appears to indicate that locusts were frequently moving offshore in the autumn, reaching west of 40° W on at least three occasions, from 8 to 17 and 25 to 29 October and from 2 to 8 November. Even with an improvement in the temporal and spatial resolution of the weather data used, the lack of detail in the locust reports prevents closer examination of the origins of the later appearances. In particular, a more precise assessment of the timing and extent of each westward incursion by locusts is hindered by the fact that the Atlantic Ocean reports depend on a remarkable coincidence between the tracks of the migrating locusts and the passage of vessels in relatively narrow commercial shipping lanes.

The invasions of the Caribbean and South America were interspersed with a movement by locusts to Britain in late October, probably in association with an eastward moving frontal depression, as with the earlier known incursions by Desert Locusts from Morocco to Portugal and to Britain (Waloff, 1946; Rainey, 1963). Using the estimated time of 60-h derived for the earlier migration to Britain in 1954 (Rainey, 1963), the first arrivals in Britain in 1988 probably started their migration on 23 to 24 October. A small 'window' of more southerly winds in the circulation of an Atlantic depression occurred at this time, between the second and third trans-Atlantic crossings, in which the migrants left the putative source areas on the easterly Trades between 19 and 23 October and again, between 27 October and 4 November. However, the source areas for the locusts invading Britain may have been further north than those identified for the swarms reaching the Caribbean and South America, since by late October there were widespread movements of swarms into Morocco, which was the source for the earlier locust invasions of Europe (Waloff, 1946; Rainey, 1963). Similarly, the end of the first locust emigrations to the Caribbean between 2 and 13 October, was marked by the passage of an eastward moving frontal depression from 14 to 17 October which transported large quantities of dust from the western Sahara and north Mauritania to north of the Pyrenees (Dessens and Van Dinh, 1990).

The trajectories depicted swarm migrations across the Atlantic within a surface layer of moist maritime air (≤ 2500 m in depth) capped by a strong temperature inversion with hot, dry air above. At times, the migrations were associated with easterly waves,

which with the strong surface convection linked to the onset of swarm migration (Rainey and Waloff, 1948), have also been associated with the eastward transport of dust in the Saharan Air Layer (SAL) above 1500 m (Carlson and Prospero, 1972; Bergametti et al., 1989; Moulin et al., 1997). There is no evidence that trajectories in the first two invasion periods were influenced by the increased wind speeds and changing wind directions associated with two tropical cyclones that moved westwards across the Atlantic Ocean (cf. Rainey, 1989; Ritchie and Pedgley, 1989). The ships reporting locusts only recorded rain showers at the times of the sightings, but not heavy seas or strong winds, which are usually associated with the passage of tropical cyclones. In addition, the timing of the passages of the cyclones did not coincide with known times of locust sightings on the Atlantic. Tropical storm Joan reached the Caribbean four to five days after the first reports of locusts, although its continued presence in the region until 23 October may have increased wind speeds towards the ends of the later migrations in the first invasion period (Ritchie and Pedgley, 1989). In contrast, the second tropical cyclone preceded the second invasion of the Caribbean and first invasion of South America by four to five days and had diminished in strength before locusts were reported in the region.

The way in which very long flights across the sea are achieved is still not clearly understood, but it is likely that the locusts that invaded the Caribbean and South America in 1988 crossed the Atlantic in swarms. Assuming a constant downwind orientation as might be expected with individual flying locusts, by adding a flight velocity of 2.5 m s^{-1} , produced the two shortest trans-Atlantic crossings in this study (93 and 96-h), but otherwise the range in trajectory durations was similar irrespective of whether flight velocity was added. In addition, Ritchie and Pedgley (1989) found that during the first invasion period, upwind trajectories with an additional flight velocity of 4.4 m s^{-1} , failed to link the Caribbean with any source areas in Africa or even reach the Cape Verde Islands.

Although a high proportion of locusts in swarms are gliding at any one time (Johnson, 1969), it is unlikely that convective up-currents over the ocean were of sufficient frequency and duration to enable a heavy insect such as a Desert Locust maintain height for any length of time without powered flight. Clearly, laboratory estimates of flight duration (Weis-Fogh, 1952, 1956) were insufficient to account for either the migrations of swarms to the Caribbean and South

America in 1988 or the earlier 1954 migration to the British Isles (Rainey, 1963). Trajectory durations of 93 to 144-h in 1988 were five to seven times longer than the maximum flight time recorded in the laboratory and those in 1954 three times longer. It is unlikely that laboratory studies using homogeneous, cultured locust populations (Weis-Fogh, 1952) would measure the full distribution of flight performance found within field populations, particularly the individuals at the extreme limits of flight endurance (Taylor, 1979; Ritchie and Pedgley, 1989). The power for locust flight is provided by the oxidation of fat and an upper limit for the potential duration of continuous flight is set by the ratio of the size of the fat content to the rate of consumption in steady flight. Summer breeding conditions may have been particularly good in 1988 (Rainey, 1989), so that the locusts may have built up large fat reserves, which sustained powered flight across the Atlantic. There is only anecdotal evidence from experienced locust officers that locusts sampled in North-West and West Africa at the end of summer 1988 had unusually high fat contents and that the migrating swarms were very mobile and unable to settle to feed for any length of time. In contrast, the invading locusts in the Caribbean showed a complete absence of fat and were very lethargic on arrival (Symmons, unpublished). Unfortunately, in spite of their high public and political profiles, Desert Locust plagues are not conducive times for research since efforts are focused on control and there are no systematic observations in 1988 on the relative sizes of individual locusts or swarms.

Displacements of locusts to areas unsuitable for breeding are infrequent, but do tend to occur towards the end of a plague (Pedgley, 1981). Desert Locust populations were substantially lower in 1989, which has been partially attributed to the substantial losses sustained due to offshore migrations, although large scale control using pesticides and lower rainfall in the seasonal breeding areas may also have contributed to the ending of the plague (US Congress, 1990). Many of the seasonal migrations of the Desert Locust occur over the sea and flights are particularly frequent over the Red Sea, Gulf of Aden and Persian Gulf (Waloff, 1960). The occurrence of Desert Locusts off the western coast of North Africa is also common, with reports in over half the years between 1942 and 1987, most of them during plagues and in the autumn. Groups or swarms of Desert Locusts have also been recorded on various occasions during the same periods in the Cape Verde Islands, the Canary Islands, Madeira and the Azores. Before 1988, however, the farthest

west Desert Locusts had been recorded was on a ship at 28°28' N, 41°33' W, 2500 km from the coast of North Africa (Waloff, 1960), although Johnson and Bowden (1973) speculated that locusts recorded over the Sargasso Sea (25°20' N, 62°30' W) in 1906 could have been Desert Locusts rather than a South American species. This study suggests that there was nothing unusual about either the prevailing weather conditions during the trans-Atlantic crossings or the offshore movement of locusts from North Africa in the late summer and early autumn. Rainey (1989) also noted the frequency with which locusts moved across the African coast and adjacent ocean and further speculated that the trans-Atlantic migrations in 1988 were a once in a few centuries coincidence of suitable weather conditions and swarms that comprised exceptional numbers of individuals with high energy reserves at the extremes of the distribution of flight performance (Taylor, 1979). The 1988 crossings of the Atlantic tend to confirm that New World species of *Schistocerca* probably evolved from ancestral Desert Locusts, which migrated on Trade winds from western North Africa and bridged the gap between continents by downwind flight.

Acknowledgements

We would like to thank Martyn Rothery for the illustrations, Ian Thomas for help with the preliminary analysis and Joyce Magor for critical appraisal of the work. This paper is an output from a project funded by the United Kingdom Department for International Development (DFID) for the benefit of developing countries. The views are not necessarily those of DFID (Crop Protection Programme: Dissemination funding).

References

- Bergametti G., Gomes L., Coude-Gaussen G., Rognon P. and Le Coustumer M.-N.: 1989, African dust observed over Canary Islands: source-regions identification and transport pattern for summer situations. *J. Geophys. Res.* **94**, 14855–14864.
- Carlson T.N. and Prospero J.M.: 1972, The large-scale movement of Saharan air outbreaks over the northern equatorial Atlantic. *J. Appl. Meteorol.* **11**, 289–297.
- Clarke J.F., Clark T.L., Ching J.K.S., Haagenson P.L., Husar R.B. and Patterson D.E.: 1983, Assessment of model simulation of long-distance transport. *Atmos. Environ.* **17**, 2449–2462.
- Coude-Gaussen G., Rognon P., Bergametti G., Gomes L., Strauss B., Gros J.M. and Le Coustumer M.-N.: 1987, Saharan dust on Fuerteventura Island (Canaries): chemical and mineralogical

- characteristics, air mass trajectories and probable sources. *J. Geophys. Res.* **92**, 9753–9771.
- Cullen M.J.P.: 1993, The unified forecast/climate model. *Met. Mag.* **122**, 81–94.
- Dessens J. and Van Dinh P.: 1990, Frequent Sahara dust outbreaks north of the Pyrenees: a sign of climate change? *Weather* **45**, 327–333.
- Ellis W.G. and Merrill J.T.: 1995, Trajectories for Saharan dust transported to Barbados using Stokes' law to describe gravitational settling. *J. Appl. Met.* **34**, 1716–1726.
- Gadd A.J.: 1985, The 15-level weather prediction model. *Met. Mag.* **114**, 222–226.
- Johnson C.G.: 1969, *Migration and Dispersal of Insects by Flight*. Methuen: London.
- Johnson C.G. and Bowden J.: 1973, Problems related to the transoceanic transport of insects, especially between the Amazon and Congo areas. In B.J. Meggers, E.S. Ayensu and D. Duckworth (eds), *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*. Smithsonian Institution Press: Washington, pp. 207–222.
- Kennedy J.S.: 1951, The migration of the Desert Locust (*Schistocerca gregaria* Forsk.). I. The behaviour of swarms. *Phil. Trans. R. Soc. Lond.* **235**, 163–260.
- Moulin C., Lambert C.E., Dulac F. and Dayan U.: 1997, Control of atmospheric export of dust from North Africa by the North Atlantic Oscillation. *Nature* **387**, 691–694.
- Pedgley D.E. (ed.): 1981, *Desert Locust Forecasting Manual, Volume 1*. Centre for Overseas Pest Research: London.
- Pedgley D.E.: 1982, *Windborne Pests and Diseases: Meteorology of Airborne Organisms*. Ellis Horwood: Chichester.
- Rainey R.C.: 1963, Meteorology and the migration of desert locusts. WMO Technical Note 54, World Meteorological Organisation: Geneva.
- Rainey R.C.: 1989, *Migration and Meteorology*. Oxford University Press: New York.
- Rainey R.C. and Waloff Z.: 1948, Desert locust migrations and synoptic meteorology in the Gulf of Aden area. *J. Anim. Ecol.* **17**, 101–112.
- Richardson C.H. and Nemeth D.J.: 1991, Hurricane-borne African locusts (*Schistocerca gregaria*) on the Windward Islands. *GeoJournal* **23**, 349–357.
- Ritchie J.M. and Pedgley D.E.: 1989, Desert locusts cross the Atlantic. *Antenna* **13**, 10–12.
- Rosenberg L.J. and Magor J.I.: 1983, Flight duration of the brown planthopper, *Nilaparvata lugens* (Homoptera: Delphacidae). *Ecol. Ent.* **8**, 341–350.
- Sayer H.: 1956, A photographic method for the study of insect migration. *Nature* **177**, 226.
- Scott R.W. and Achtemeier G.L.: 1987, Estimating pathways of migrating insects carried in atmospheric winds. *Env. Entomol.* **16**, 1244–1254.
- Stemshorn B.: 1989, Desert Locusts in the Caribbean. In B. Stemshorn (ed.), Proceedings of a Regional Meeting Port of Spain, Trinidad and Tobago November 16, 1988. IICA Miscellaneous Publication A2/TT-89-01, Inter-American Institute for Cooperation on Agriculture, Trinidad and Tobago.
- Taylor R.A.J.: 1979, A simulation model of locust migratory behaviour. *J. Anim. Ecol.* **48**, 577–602.
- U.S. Congress: 1990, A plague of locusts – special report. U.S. Congress Office of Technology Assessment, Washington.
- Waloff Z.: 1946, A long-range migration of the desert locust from southern Morocco to Portugal, with an analysis of concurrent weather conditions. *Proc. R. ent. Soc. Lond. Series A.* **21**, 81–84.
- Waloff Z.: 1960, Some notes on the desert locust and on its occurrence at sea. *The Marine Observer* **30**, 40–45.
- Waloff Z.: 1966, The upsurges and recessions of the desert locust plague: an historical survey. Anti-Locust Memoir No. 8, London.
- Waloff Z.: 1972, Orientation of flying locusts, *Schistocerca gregaria* (Forsk.). *Bull. ent. Res.* **62**, 1–72.
- Weis-Fogh T.: 1952, Fat combustion and metabolic rate of flying locusts (*Schistocerca gregaria* Forskål). *Phil. Trans. R. Soc. Lond.* **237**, 1–36.
- Weis-Fogh T.: 1956, Biology and physics of locust flight. II. Flight performance of the desert locust (*Schistocerca gregaria*). *Phil. Trans. R. Soc. Lond.* **239**, 459–510.
- Weis-Fogh T.: 1976, Energetics and aerodynamics of flapping flight: a synthesis. In R.C. Rainey (ed.), *Insect Flight*. Seventh Symposium of the Royal Entomological Society of London. Blackwell Scientific Publications: Oxford, pp. 48–72.
- Whittlestone S., Robinson E. and Ryan S.: 1992, Radon at the Mauna Loa Observatory: transport from distant continents. *Atmos. Environ.* **26A**(2), 251–260.

