Rainfall as a factor in the geographical distribution of the desert locust breeding areas, with particular reference to the summer breeding area of India and Pakistan.

by

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Thesis submitted for the degree of Doctor of Philosophy in the University of Edinburgh.

Anti-Locust Research Centre,
London.
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INTRODUCTION

A. THE INFLUENCE OF ENVIRONMENTAL FACTORS ON THE LIFE CYCLE OF THE DESERT LOCUST. (*Schistocerca gregaria* Forskal)

The desert locust is a large insect weighing 1-3 gm. with a wing span of 10-15 cm. Its eggs are laid in moist sandy soil from which the water necessary for their development is absorbed. After hatching the hoppers moult 5 or occasionally 6 times before reaching the adult, fully winged stage. After a short time any swarms which have formed are ready to migrate. They move downwind and in this way reach areas of low level convergence of winds where precipitation is likely to occur. In these areas maturation usually takes place almost immediately and the cycle begins again.

There are, however, two exceptions to the latter part of the cycle. One, where the area in which fledging took place is still receiving rain when maturation may take place *'in situ'* and two successive generations be produced in the same area. The second takes place where swarms arrive in an area during the rainy season but maturation does not take place immediately and immature swarms remain in the area for some months before the cycle begins again.

The desert locust is adapted to life within the wide range of climatic environments found in its widespread distribution area. The length of time taken to pass through the stages outlined above varies considerably with
the differing combinations of environmental factors such as temperature, and possibly humidity, light and food, as well as the density of the locusts themselves. These complicated and continuously varying environmental conditions have not been reproduced in the laboratory and thus the effects of each of these many factors are still not fully known and understood. The following account outlines the present knowledge of the effects of environmental factors on the life cycle of the desert locust.

1. Oviposition.

Kennedy (1949) observed that for the African migratory locust (Locusta migratoria migratorioides R. & F.) oviposition could be divided into three stages:-

1. **Probing**: that is, working of the ovipositor against the substrate with the abdomen bent at right angles but not yet extended.

2. **Digging**: that is, continued working of the ovipositor valves while the abdomen extends and makes twisting movements.

3. **Oviposition proper**: that is, extrusion of froth and eggs to form an egg pod as the abdomen is retracted out of the hole.

It has been found (Popov 1958, etc.) that these stages are also characteristic of oviposition by the desert locust. Probing and digging follow copulation and are the means by which suitable egg sites are found. Probing was observed by Popov (ibid) on many types of soil and it apparently resulted in the rejection of hard, compact surfaces, for digging was restricted to soft, sandy soils. Oviposition did not always follow digging, suggesting that the final
test of the suitability of the soil for oviposition was made during this process. Popov's observations led him to believe that not only environmental conditions but also the physiological condition of the female locusts played a part in the rejection of some of the bore holes that had been made by digging.

During one particular series of laboratory experiments Popov (ibid) found that although 54 bore holes were made in dry sand, it contained no egg-pods, however in the moist sand presented to the locusts at the same time there were 15 bore holes and 19 egg-pods.

These results led him on to further experiments in which he demonstrated that the desert locust showed a preference for laying in sand which had a dry surface layer. During these experiments a total of 87 egg pods were laid, 57 where the sand was dry on the surface and 30 when the sand was moist throughout. These results were tested statistically, and proved to be significantly different.

In the laboratory eggs were laid only if they could be placed completely in moist soil, otherwise they were retained for up to 72 hours and were then deposited on the floor of the cage (Popov ibid). These points are dealt with fully in chapter 1 on oviposition and soil moisture.

The reproductive activities are sometimes interrupted by sheltering and roosting; field observations and laboratory experiments have been carried out to determine the conditions under which these interruptions occur.
Ballard et al (1932) and Popov (ibid) have noted sheltering by adult locusts during rain under field conditions. Hussain and Mathur (1946) simulated rainfall in the laboratory and sheltering but no interruption of sexual activity was observed. Heat, cold and darkness were also thought by Popov (ibid) to induce sheltering and roosting. For when at oviposition sites in east Africa a soil surface temperature (measured with a mercury in glass angle thermometer) of 43°C was reached, adult locusts began to shelter in the shade of bushes or to climb on to the branches and roost until later in the day, when the soil surface temperature had fallen. The first locusts to seek shelter were the marching pairs, followed by those probing and lastly by the ovipositing locusts. It should be noted that a temperature gradient amounting to 16°C can exist at noon between the sand's surface and the air 6 mm. above that surface (Geiger 1950). Thus the temperature of 43°C measured by laying a thermometer on the ground would probably be lower than that of the actual soil surface, for there would have been a temperature gradient between the lower surface of the bulb in contact with the surface of the sand, and the upper surface of the bulb in contact with the cooler air.

Variations in the temperature of the soil surface in the vicinity of egg-bearing swarms played a part in the selection of egg-sites. During the middle of the day oviposition was occasionally seen by Popov (ibid) to occur
in the cooler areas, on the slopes facing away from the sun or in the light shade cast by small bushes, near where the locusts had been sheltering. This use of the cooler sites was only seen to operate when the soil surface temperature was above 39°C and less than 43°C, at which point laying was usually suspended and sheltering and roosting began.

In the morning and evening the locusts move onto the warmer, sunward facing slopes and bask. During this activity they present their sides to the sun and thereby absorb the maximum possible radiation. Oviposition frequently followed basking particularly in the evening (Popov ibid). Basking continued during his observations until the soil surface temperature reached 24–26°C in the morning and began in the evening when the soil surface temperatures were 34–36°C.

When the soil texture and moisture conditions were suitable for oviposition over a wide area Popov noted an association between basking and oviposition sites. Sometimes these open sunward facing slopes had dried out and under these conditions, after basking the locusts moved to the hollows where moisture had been conserved, before suitable laying sites were found.

Some data on the temperatures under which oviposition occurred have been noted. Mass oviposition in Iran was seen at air temperatures between 22 and 33°C (Popov 1954). In east Africa the upper limit of temperature during oviposition was:— soil surface temperature 43–46°C which corresponded to air temperatures of 28–34°C. The lowest
**TABLE 1:** Temperatures at which oviposition has been observed.

<table>
<thead>
<tr>
<th>FIELD DATA</th>
<th>LABORATORY DATA</th>
<th>NOTES and SOURCES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temp. °C</td>
<td>Soil surface temp. °C</td>
<td>Soil temp. °C at depth 7.5-10 cm,</td>
</tr>
<tr>
<td>22 - 33</td>
<td>23 - 46</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>25 - 29</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20 - 23</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
air and soil surface temperatures at which oviposition was observed was 21°C (Popov 1958).

Husain and Ahmad (1936) examined experimentally the temperature range over which oviposition would occur. The upper limits they obtained by heating the soil from below thus obtaining a temperature gradient the reverse of that occurring in the field. Oviposition occurred when the air temperature varied from 25–36°C when the soil surface temperature was 30–42°C the temperature at which the eggs were deposited was 40–48°C. It should be noted that none of these eggs hatched. The authors in a later experiment showed that eggs 1–2 days old exposed to a temperature of 47°–47.5°C for 2 hours did not develop when subsequently incubated at 30–33°C, neither did eggs which were kept for eight hours at 46–46.5°C although a 2 hour period at this temperature was not fatal. Thus it seems likely that the failure of the eggs to hatch in their previous experiment was caused by high temperatures.

In other experiments the locusts were presented with a range of soil temperatures which varied between 0° and 30°C at a depth of 7.5–10 cm, i.e. at the level where the eggs were usually deposited. The eggs were deposited where the soil temperatures were between 25.5° and 29°C. When the choice of temperatures was restricted further the eggs were deposited where the temperature was between 20° and 23°C, the highest soil temperatures available.

Rao (1960) records oviposition occurring in a large
Fig. 1. The changing weight of eggs of the desert locust incubated at 27°C. (after Shulov, 1952)
field cage at Pasni (Baluchistan) at a soil surface temperature of 25°C measured with the thermometer lying horizontally and covered thinly by soil. He also noted "digging for oviposition" occurring when the soil surface temperature was 18°C.

Table 1 summarises the data available on the temperature at which oviposition has been seen both in the field and in the laboratory and indicates that the temperatures under which oviposition has been observed in the field correspond closely to the range of temperatures found suitable experimentally in the laboratory and it seems likely that oviposition by the desert locust is restricted by certain soil surface temperatures. As yet these have not been measured very accurately; but the limiting temperatures measured by the methods noted above are 18°C and 46°C. It seems that there must also be a minimum amount of moisture present in the soil before normal oviposition will occur.

ii. Egg Development.

The eggs of the desert locust are laid containing insufficient water for their development. This is obtained from the moist sand in which they are laid. Shulov (1952) demonstrated the increasing weight of eggs kept in moist sand at 27°C during their incubation period. (see fig.1). Hunter-Jones (in preparation) has also shown the pattern of water uptake by eggs of the desert locust from sand moistened by varying amounts of water when incubated at 28°C.
Fig. 2a. Changes in weight of developing eggs of the desert locust when incubated in sand containing 0.6, 1.3, 2, 10, 20, 25 cc water to 100 gm sand. (after Hunter-Jones in preparation).
Fig. 2b. Eggs of the desert locust kept in moist sand (10cc water to 100gm sand) for part of the incubation period and then transferred to sand containing only 0.6cc water to 100gm sand. (broken line) (after Hunter-Jones in prep)
His results (fig. 2a) show that the eggs were able to hatch satisfactorily except where the soil was water-logged (i.e. when 30 cc. water added) or when the moisture content was as low as 0.6 cc. in 100 gm. of sand. In the former case the eggs almost certainly died through lack of oxygen. In the latter there was a gradual increase in weight over the first 10 days which differed in pattern from that which occurred when the eggs hatched. Partially developed eggs were able to complete their development in sand containing this amount of moisture, their hatching weight reflecting the length of time spent in this drier sand (fig. 2b). This would suggest that the water at this concentration was available to the eggs, but that if they had not initially been in moister sand, the pattern of water uptake was abnormal and they failed to hatch. The length of the incubation periods during these experiments varied from 17-19 days.

Husain, Ahmad and Mathur (1941) examined the influence of soil moisture on the length of the incubation period of the eggs of the desert locust. They used sandy, loam, clay-loam and clay soils for their experiments. These soils were first oven dried at 60°C and were then placed in a dessicator for two days at a relative humidity of 100%. In this way the soils were moistened to what the authors termed "maximum hygroscopic moisture." Eggs were then placed in these soils, to some of which were added known quantities of water. They were then incubated at known room temperatures in a dessicator in which the air was always
TABLE 2: The influence of soil moisture on the development of eggs. (after Husain, Ahmad & Mathur 1961.)

<table>
<thead>
<tr>
<th>Soil type</th>
<th>No</th>
<th>% moisture added</th>
<th>Date of oviposition</th>
<th>Date of moistening</th>
<th>Date of hatching</th>
<th>Incubation period (days)</th>
<th>Temp. during experiment</th>
<th>Expected incubation period at these temperatures (after Rao, 1960.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sandy</td>
<td>a</td>
<td>Saturated</td>
<td>4 Aug.</td>
<td>-</td>
<td>16 Aug.</td>
<td>12</td>
<td>34</td>
<td>13.14</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>8.4</td>
<td>do</td>
<td>-</td>
<td>17 Aug.</td>
<td>13</td>
<td>34</td>
<td>13.14</td>
</tr>
<tr>
<td></td>
<td>c</td>
<td>4.2</td>
<td>do</td>
<td>-</td>
<td>18 Aug.</td>
<td>14</td>
<td>34</td>
<td>13.14</td>
</tr>
<tr>
<td></td>
<td>d</td>
<td>Max. hyg.</td>
<td>do</td>
<td>-</td>
<td>21 Aug.</td>
<td>17</td>
<td>34</td>
<td>13.14</td>
</tr>
<tr>
<td>Sandy</td>
<td>a</td>
<td>4.6</td>
<td>4 Sept.</td>
<td>-</td>
<td>17 Sept.</td>
<td>13</td>
<td>34</td>
<td>13.14</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>4.6</td>
<td>do</td>
<td>-</td>
<td>17 Sept.</td>
<td>15</td>
<td>34</td>
<td>13.14</td>
</tr>
<tr>
<td></td>
<td>c</td>
<td>2.25</td>
<td>do</td>
<td>-</td>
<td>19 Sept.</td>
<td>15</td>
<td>34</td>
<td>13.14</td>
</tr>
<tr>
<td></td>
<td>d</td>
<td>2.25</td>
<td>do</td>
<td>-</td>
<td>23-25 Sept.</td>
<td>23-25</td>
<td>33.6</td>
<td>13.14</td>
</tr>
<tr>
<td>Sandy</td>
<td>a</td>
<td>Air dry</td>
<td>27 Apr.</td>
<td>14 May</td>
<td>25 May</td>
<td>28</td>
<td>30</td>
<td>Constant</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>control*</td>
<td>do</td>
<td>14 May</td>
<td>17</td>
<td></td>
<td>Constant</td>
<td>-</td>
</tr>
<tr>
<td>Sandy</td>
<td>a</td>
<td>Hyg 80% RH</td>
<td>8 May</td>
<td>21-May</td>
<td>31 May</td>
<td>23</td>
<td>35</td>
<td>Constant</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>control*</td>
<td>do</td>
<td>21-May</td>
<td>13</td>
<td></td>
<td>Constant</td>
<td>-</td>
</tr>
<tr>
<td>Loam</td>
<td>a</td>
<td>30</td>
<td>18 July</td>
<td>-</td>
<td>31 July</td>
<td>13</td>
<td>36.1</td>
<td>Constant</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>20</td>
<td>do</td>
<td>-</td>
<td>31 July</td>
<td>13</td>
<td>36.1</td>
<td>Constant</td>
</tr>
<tr>
<td></td>
<td>c</td>
<td>20</td>
<td>do</td>
<td>-</td>
<td>31 July</td>
<td>13</td>
<td>36.1</td>
<td>Constant</td>
</tr>
<tr>
<td></td>
<td>d</td>
<td>5</td>
<td>do</td>
<td>-</td>
<td>3-4 Aug.</td>
<td>16-17</td>
<td>36</td>
<td>13.14</td>
</tr>
<tr>
<td></td>
<td>e</td>
<td>Max. hyg.</td>
<td>do</td>
<td>-</td>
<td>6 Sept.</td>
<td>50</td>
<td>34.9</td>
<td>13.14</td>
</tr>
<tr>
<td>Clay loam</td>
<td>a</td>
<td>13.3</td>
<td>4 Sept.</td>
<td>-</td>
<td>24 Nov.</td>
<td>81</td>
<td>28.4</td>
<td>19.4 26.9</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>6.6</td>
<td>4 Sept.</td>
<td>24 Nov.</td>
<td>24 Nov.</td>
<td>81</td>
<td>28.4</td>
<td>19.4 26.9</td>
</tr>
<tr>
<td></td>
<td>c</td>
<td>6.6</td>
<td>do</td>
<td>24 Nov.</td>
<td>81</td>
<td></td>
<td>28.4</td>
<td>19.4 26.9</td>
</tr>
<tr>
<td>Clay</td>
<td>a</td>
<td>18.7</td>
<td>7 Aug.</td>
<td>-</td>
<td>19 Aug.</td>
<td>12</td>
<td>34</td>
<td>13.14</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>9.8</td>
<td>do</td>
<td>-</td>
<td>21 Aug.</td>
<td>14</td>
<td>34</td>
<td>13.14</td>
</tr>
<tr>
<td></td>
<td>c</td>
<td>5.3</td>
<td>do</td>
<td>-</td>
<td>6 Sept</td>
<td>30</td>
<td>32.5</td>
<td>14.7 14.7</td>
</tr>
<tr>
<td></td>
<td>d</td>
<td>3.2</td>
<td>do</td>
<td>-</td>
<td>6 Sept</td>
<td>30</td>
<td>32.5</td>
<td>14.7 14.7</td>
</tr>
<tr>
<td></td>
<td>e</td>
<td>Max. hyg.</td>
<td>do</td>
<td>-</td>
<td>5 Nov.</td>
<td>30</td>
<td>32.5</td>
<td>14.7 14.7</td>
</tr>
</tbody>
</table>

* moist sand, moisture content not stated.
saturated with moisture unless otherwise stated. Their results are given in Table 2 and show how the length of the incubation period was lengthened when the moisture was in short supply. To this table, I have added the length of the incubation periods given by Rao (1960) for the temperatures quoted by Husain, Ahmad and Mathur.

In the first two experiments when sand had been used all the eggs hatched without the addition of further moisture, indicating that the variations in temperature must have made water of condensation available for absorption by the eggs. In the other experiments using sand when the control eggs hatched moisture was added to any unhatched experimental eggs, with the result that hatching occurred some 10 or more days later.

In the experiments where other types of soil were used, the eggs in the dishes containing only a low percentage of additional water did not always hatch unless additional moisture was added. The extension of the incubation periods above that usual for the temperatures of the experiments was greater when clay-loam soil was used, when the incubation period was 81 days (normal 19-27 days).

These results suggest that the eggs of the desert locust are able to absorb any moisture in a sandy soil other than hygroscopic moisture, but that this is not so when the eggs are in 'heavier' soils. The amount of additional water required increases with the increasing 'heaviness' of the soil. It is of course possible that the
Fig. 3. Incubation period in relation to soil temperature at 4 inch [10cm] depth showing the difference in value for each rise of a degree Celsius. (after Rao, 1960)
method utilised for producing soils containing "maximum hygroscopic moisture" was not an effective one for these 'heavier' soils for no direct measurements of moisture content were made.

The effects of temperature on the incubation period of the desert locust were demonstrated by Rao (1960). In a series of experiments carried out between 1932 and 1937, the temperature of the moist sandy soil at a depth of 10 cm. was measured during the development of the eggs. His results show that the length of the incubation period increased as shown in fig.3 from 13 days at 34°C to 72 days at 19°C. Similar results were obtained by Husain and Ahmad (1936) and Shulov (1952) and Hamilton (1950).

Thus it can be seen that the eggs of the desert locust, having been laid in suitably moist soil, absorb from it the moisture necessary for their development. The length of their incubation period is largely dependent on temperature, but particularly when in soils (other than sand) with a low moisture content their incubation period may be considerably extended.

iii. Hopper Development.

Early field records quoted by Bodenheimer (1929) and Husain and Ahmad (1936) from widely differing areas and seasons of the length of hopper development varied greatly from 37-153 days (see Table 3).

Experiments conducted by Husain and Ahmad (ibid) showed the effect of different constant temperatures on the length
**TABLE 3: Records of the duration of the hopper period.**

<table>
<thead>
<tr>
<th>Author</th>
<th>Country</th>
<th>Duration of hopper period (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vosseler</td>
<td>East African Steppes</td>
<td>50</td>
</tr>
<tr>
<td>Vosseler</td>
<td>East African Mountains</td>
<td>60-70</td>
</tr>
<tr>
<td>King</td>
<td>Sudan</td>
<td>40-50</td>
</tr>
<tr>
<td>Lellement</td>
<td>Algeria</td>
<td>44-53</td>
</tr>
<tr>
<td>Official</td>
<td>Morocco</td>
<td>40</td>
</tr>
<tr>
<td>Gough</td>
<td>Egypt</td>
<td>44</td>
</tr>
<tr>
<td>Bücher</td>
<td>Palestine</td>
<td>42-56</td>
</tr>
<tr>
<td>Regnier</td>
<td>N.W. Africa</td>
<td>37-40</td>
</tr>
<tr>
<td>Bodenheimer</td>
<td>Palestine</td>
<td>42</td>
</tr>
<tr>
<td>Ballard et al</td>
<td>Egypt</td>
<td>39-153</td>
</tr>
</tbody>
</table>
of hopper development. It was found to vary from 61-63 days at 24°C to 20-21 days at 36°C. At a temperature of 44°C only a few hoppers reached the adult stage after 27 days, i.e. longer than at lower temperatures. Greatly increased periods of development of up to 161 were obtained both by Husain and Ahmad (ibid) and Rao (1960) when breeding hoppers under semi-natural conditions during winter months when the temperature was frequently below 19°C, which has been indicated as a threshold for development by Husain and Ahmad (ibid). Experiments by Husain, Ahmad and Mathur (1941) showed that where green food was available, low humidity did not prolong the duration of the hopper stages as had been suggested by the work of Hamilton (1936 and 1950). Dudley (1960) who was able to use an artificial diet which enabled the humidity to be more fully controlled than before also found that humidity did not affect the length of the hopper stages.

iv. Flight Activity.

After the final moult the fledgling is only capable of descending flight until about a week later when the development of its flight muscles and the hardening of its wing structure is completed. From this point flight activity is a characteristic feature of the adult desert locust.

Waloff and Rainey (1951) considered the factors (air temperature, sunshine, wind, rain, gregarious stimulation, fatigue and feeding) which affect flight activity. They
<table>
<thead>
<tr>
<th>Air Speed km/hr</th>
<th>Method</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><strong>A. Determinations in the Laboratory.</strong></td>
</tr>
<tr>
<td>14-16</td>
<td>initial speed</td>
<td>on a roundabout at 25-35°C.</td>
</tr>
<tr>
<td>11</td>
<td>average speed</td>
<td>at 25-35°C.</td>
</tr>
<tr>
<td>8-13</td>
<td>range</td>
<td>on a roundabout at 25-31°C for 4-5hr.</td>
</tr>
<tr>
<td>10.8</td>
<td>average speed</td>
<td>at 25,30, &amp; 35°C for 4-5hr</td>
</tr>
<tr>
<td>9-13</td>
<td>range</td>
<td>on a roundabout</td>
</tr>
<tr>
<td>10</td>
<td>average speed</td>
<td>attached to flight balance in wind tunnel</td>
</tr>
<tr>
<td>9-23.4</td>
<td>extreme values</td>
<td></td>
</tr>
<tr>
<td>10.8-18</td>
<td>average range</td>
<td></td>
</tr>
<tr>
<td>11.5</td>
<td>average speed</td>
<td></td>
</tr>
<tr>
<td>B. Estimations in the field.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14.5</td>
<td>unrecorded</td>
<td></td>
</tr>
<tr>
<td>29</td>
<td>timed flight of 200 metres in still air</td>
<td></td>
</tr>
<tr>
<td>16.5</td>
<td>observer holding direct reading anemometer keeping pace with locust at 29.5°C.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>between 11&amp;18...same method</td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>visual estimate by 2 observers</td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>course of track observed in mirror; wind speed and direction measured. Temperature 31-32°C.</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>photographic technique of double exposure</td>
<td></td>
</tr>
</tbody>
</table>

**Source:**
- Krogh and Weis-Fogh (1952)
- Weis-Fogh (1952)
- Wooten and Sawyer (1954)
- Lepinay (1928)
- Rungs (1945)
- Gunn, Perry et al (1948)
- Rainey & Waloff (1951)
- Rainey Waloff & Sayer (in prep)
concluded that in the range of environmental conditions encountered that particularly at low air temperatures, sunshine was of importance in the development of flight activity. In the absence of sunshine, the body temperature of the locusts approximates to that of the air and this temperature then becomes a dominant factor in controlling flight activity. It was through the part they play in regulating the body temperature of locusts that these factors were thought to be effective.

Krogh and Weis-Fogh (1952) found by laboratory determinations that in the absence of heating radiation sustained flight activity took place at air temperatures ranging from 22-37°C with optimum conditions from 25-35°C. Gunn, Perry et al (1948) observed flight activity in the field among locusts with similar body temperatures (20-40°C).

Various determinations of the air speed of locusts have been made in the laboratory. Krogh and Weis-Fogh (1952) and Weis-Fogh (1952 and 1956) concluded that during steady horizontal flight it would probably be 10-13 km/hr, although initially a higher speed of 14-16 km/hr was usual. Wootten and Sawyer (1954) obtained air speeds of 9-23 km/hr with an average value of 11.5 km/hr. Several estimates have been made by various methods under field conditions (see Table 4).

v. Swarm Movements.

The determination of the air speed of desert locusts under controlled conditions in the laboratory vary from
8-23 km/hr. These results suggest that a swarm of locusts uniformly orientated into the wind would not be able to make headway against a wind of more than about 23 km/hr. and that the direction of displacement at wind speeds higher than this would necessarily be down or across wind.

Observations from slow flying light aircraft (Rainey and Sayer 1953) showed that swarms were composed of a large number of groups of locusts. Within each group the locusts were uniformly orientated but a wide diversity of orientation was observed between groups. These observations were later confirmed by a photographic technique using double exposures (Rainey, Waloff and Sayer in preparation).

A study of over 40 examples where the direction of displacement of the swarms had been established by successive fixes and the direction and speed of the wind had been recorded, led Rainey (in preparation) to conclude:

"that despite the uniformity of orientation so conspicuously exhibited within the individual groups of flying locusts, both the direction and maximum speed of displacement observed in flying swarms reflect an effectively random overall orientation of the flying locusts in the swarm as a whole."

Studies by Rainey (in preparation) of the geographical displacement of over 40 swarms with which contact had been maintained by aircraft, led to their classification into four types.

1) Progressive, systematic swarm movement in which there was a constancy of more than 75% over periods of a few hours to five days. These were associated with quasi-stationary
wind-fields.

2) Marked changes in the direction of swarm movement where the constancy was less than 75%. These were associated with marked changes in wind direction.

3) Complex changes in the direction of swarm movement in which the swarm crossed its previous track. These were associated with changes in wind direction both in lowland and mountainous areas.

4) Quasi-stationary flying swarms, when despite conspicuous flight activity the roosting sites of the swarm for several successive days overlapped. Both of the examples studied so far occurred in the mountains and are thought to be connected with the anabatic flow which takes place during the day in such areas.

These findings were later used by Aspliden and Rainey (in preparation) to study the movements during the period May 1954–May 1955, which could be established from the progressive day to day changes in the area occupied by swarms. It was found that:

1. the long range progressive displacements of swarms, which had taken place in periods of, from 5 days to 2 months, were associated with:

   a. quasi uniform wind fields such as the trade winds:

   b. extra tropical depressions, when the movement proceeded intermittently during the periods when warmer winds were blowing from the appropriate sector:

   c. during the seasonal displacements of the inter-tropical
convergence zone (ITCZ).

2. Periods when the swarms remained quasi-stationary for two to four months were associated with:
   a. opposing wind fields such as the convergent low level wind-field of the ITCZ, the opposing NW and SE low level wind currents characteristic of the winter conditions in the Red Sea Basin; and the on-shore sea breeze which opposed the light off-shore more general wind flow during the winter in Kathiawar, India:
   b. low temperatures which in areas such as southern Morocco most probably reduced flight activity;
   c. mountainous areas such as parts of Algeria and eastern Africa where as well as low temperatures the local anabatic circulation probably played an important part in reducing the progressive movement of swarms.

   During the study of Aspliden and Rainey (ibid) it was established that swarms move downwind during the periods of long range and progressive movement over distances of 600-3500 km. These swarms eventually arrive in areas of low level convergent wind flow. As was noted above, the swarms remain quasi-stationary in such areas which are subject to precipitation during the oscillations of the frontal systems which accompany the passage of disturbances. In many but not all of these areas the arrival of the swarms is quickly followed by maturation and oviposition among them.

vi. Sexual Maturation.

An association between precipitation and breeding has long
been recognised (Maxwell-Darling 1934) considered that

"while atmospheric humidity causes sexual maturation, rainfall is necessary for oviposition."

He based these conclusions on his observations of locusts none of which laid in the field until rain had fallen; and on his experiments with immature locusts which were kept in cages and jars with varying combinations of natural (from the field) and green vegetation and dry and wet sand. The air temperatures of both the cages and the jars was similar but the humidity in the jars varied between 40 and 50% whereas that in the cages was below 20% for all but 3 days of the experiment. The locusts in the cages did not become sexually mature until the rains came, at which time sexual maturation was also taking place in the field. However, maturation took place earlier in the jars and Maxwell-Darling concluded that the higher atmospheric humidity was the factor that had induced maturation. Noting that the locusts in the jars had eaten four times as much food as those in the cages he thought that the influence of the humidity on maturation might have been indirect and connected with the increased feeding observed.

Rao (1960) following his observations on the solitary populations in India and Pakistan also noted the association between rainfall and breeding.

"Breeding occurred only when there was rainfall sufficient to bring about a fairly deep penetration of moisture in sandy soils. In cases where locusts were already fairly mature at the time of the occurrence of rain, eggs were laid almost immediately, while in other
Fig. 4. Pre-oviposition period at constant temperatures. (after Husain and Ahmad, 1936)
cases sex-maturation was apparently hastened thereby."

It is frequently noted as in Norris (1957) that

"Schistocerca under natural conditions breeds when it meets with rainfall, in the absence of which it remains immature for long periods. This has usually been considered to be the result of direct inhibition of reproduction by low humidity or its effect on the food supply."

She had, however, observed retardation of maturation which took up to 113 (normal 21-28 days) days during conditions of long photoperiod or during rearing at low density. (Norris 1952 and 1957). There are, however, conditions under which maturation in the field is retarded although precipitation is occurring and the photoperiod is not long. These conditions are present in the autumn and winter in the northern area of spring breeding which extends throughout the belt affected by the westerly depressions which cause autumn and, or winter and spring precipitation from Morocco through the Middle East to Pakistan and India. In these areas swarms remain immature for up to 6 months. In this area it is probable that the low temperatures at this season inhibit maturation for Rao (ibid) found that:-

"in winter and early spring temperatures are too low to allow of breeding, and it is only when the daily mean rises to above 20^0C that locusts manifest signs of reproductive activity in north-west India."

Hussain and Ahmad (1936) examined the rate of sexual maturation at varying temperatures and found that the pre-oviposition period which they used to indicate the time taken to reach maturity varied according to temperature.
Fig. 4 shows their results for constant temperatures ranging from 27°-40°C. During the winter locusts which had fledged between August and November were reared in a laboratory at room temperature which "remained below 18°C" during December and January. Oviposition began when the "maximum temperature rose to about 21°C." Unfortunately no other details about the room temperature were given. The pre-oviposition period of these locusts varied from 87-192 days (average 133 days). The delay in maturation produced under these conditions of low temperature was probably similar to that which was taking place in the field during the same period.

Hamilton (1950) examined the effects of relative humidity at different constant temperatures on the rate of sexual maturation. Apart from partially drying the food to counteract its effect on the relative humidity in the cages no control of the food either quantitative or qualitative was made. Hamilton concluded from his results that for each of the temperatures he used 26.5, 32 and 38°C, the optimum relative humidity lay between 65 and 70%. Away from the optimum conditions of humidity, maturation time increased. However, whereas at high humidities the length of life decreased it did not do so at low humidities. Hamilton (1936) was able to keep adults immature at 32°C and 30% RH for 98 and 123 days before placing them in a humidity of 75% when they became mature within a fortnight.

During other experiments using alternating conditions, the time taken to reach maturity was shorter than when the
conditions had been constant (Hamilton 1950) Hamilton concluded therefore that maturation was stimulated by alternating conditions.

Although these results suggest that atmospheric humidity plays an important part in maturation, it has been shown that in the presence of succulent food (such as green cabbage leaves) maturation times are not retarded even when the cage relative humidity was as low as 35% (Husain, Ahmad and Mathur 1941). Norris (1952) also found no evidence of any effect of relative humidity affecting maturation time during experiments when the mean relative humidity varied between 34 and 70%. In these experiments unlike those of Hamilton's fresh grass was present which raised the relative humidity near it from 5 to 12%.

The recent work of Dudley (1961) was carried out under more rigidly controlled constant temperature, humidity, light and food conditions and he concluded from his observations that:

"...it seems clear that the failure to reproduce on the part of the locust resulted from the constant temperature, for tests on the other factors have shown that, individually each was not concerned. Although constant temperature is, therefore, believed to be of prime importance in producing this result, it is nevertheless possible that other factors might have contributed and that the result could have been caused by constancy of conditions in general. It is, however, beyond the scope of the present work to investigate this latter possibility."

He also found that the conditions under which the hoppers had developed affected their rate of maturation as adults, as
did the length of time in which the female locust had been in the constant environment before being placed in conditions known to end the delay. Male locusts reared under the constant conditions required either stimuli from the physical environment when fully grown or, in certain circumstances, particular feeding conditions for sexual maturation to be completed. In the laboratory either stimulus on its own was sufficient to cause maturation, but Dudley felt that both stimulate maturation in the field. The food factor involved was found not to be one of moisture intake alone but to be connected with some constituent of the grass which either was destroyed or taken in insufficient quantities when the grass was dried. He also found evidence as had Norris (1957) that there was a seasonal variability in the grass which increased the rate of maturation in the spring.

Among female locusts the delay could be broken by the same stimuli as for the males, and in addition the stimulus of copulation caused maturation. However, until about 30 days after fledging when resorption of their eggs had commenced, a delay was noted after transference to a suitable environment which was only shortened by copulation with mature yellow males.

It would appear then that in the field maturation is consistently delayed both under dry-season and winter conditions. Laboratory experiments to investigate this problem have consisted in subjecting the locusts to differing but usually approximately constant conditions
of temperature and relative humidity. They have shown that in fact low temperatures do reduce the rate of sexual maturation and that grass which is dry also inhibits maturation but in a way as yet unknown. Delays have been caused by constant conditions probably by constant temperature and maturation followed when these conditions were changed. In the field conditions as constant as those required to cause this delay never occur however maturation does follow the sudden environmental changes which accompanies the onset of the rains in some breeding areas.

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B. INTRODUCTION TO THE PRESENT STUDY.

i. Historical Background.

Plagues of locusts are one of the world's oldest entomological problems. Invasions by the desert locust can at times cause localised devastation in a large part of arid and semi-arid Africa and south-west Asia. In Morocco in one season alone, crop damage amounted to 13 million U.S. dollars (Vayssiére 1954). In western Eritrea in September 1958, late instar hoppers and fledglings caused the loss of 43,000 tons of cereals, which expressed in other terms amounts to a year's food supply for 170,000 people (East Africa High Commission 1961, and Bullen unpublished).

It was not until about thirty years ago that a systematic attempt was made to collect information about locust distribution. This followed the discovery by Uvarov and Faure (Uvarov 1921 & 1928) that the locusts which in the solitary phase did relatively little harm to crops, underwent gregarisation under certain conditions and greatly increased in numbers changed into the recognisably distinct gregarious phase; the resultant swarms causing much damage to crops. Until that time the two phases had been thought to be unconnected and research on locusts and methods for their control had only taken place on the gregarious phase during times of plague.

In April 1929, about a year after an invasion by the
desert locust of the Anglo-Egyptian Sudan, Kenya and Tanganyika, a locust sub-committee was formed by the late Earl of Balfour, Chairman of the Committee of Civil Research. Two years later this committee was absorbed by the Economic Advisory Council and became the Committee on Locust Control of that Council. From the beginning it was decided to collect information about all the infested territories of Africa and Western Asia in an attempt to locate the permanent breeding areas and migration routes of the desert locust. With this end in mind Sir Boris Uvarov (then senior assistant in charge of locust investigations at the Imperial Bureau of Entomology) wrote 'Instructions for Observations on Locusts' (Uvarov 1930) setting out the means of distinguishing between the types of locusts likely to be seen and indicating by a series of questions the information about the environment and behaviour of locusts that would be of value to entomologists. This pamphlet was widely distributed in all the affected territories and the information requested was immediately forthcoming. Thus the collection of documents and manuscripts now held by the Anti-Locust Research Centre was begun.

At the First International Anti-Locust Conference, Rome, 1931, it was decided:

"1) That all information on locusts in Africa and Western Asia should be centralised in a single institution in Europe;

2) That the Imperial Institute of Entomology should be

1 Now the Commonwealth Bureau of Entomology. In 1945 a separate organisation The Anti-Locust Research Centre was formed to continue the work on locusts.
A possibly distinct race of Desert Locust

Fig. 5. The distribution area of the desert locust.
adopted as the international centre for locust research, because it had the experts, documentation and collections;

3) That monthly reports on locusts should be prepared, separately for each species, according to an agreed form, accompanied by maps showing various locust activities by special symbols, and submitted by each country, or territory to the Centre. (Uvarov 1951)

After this agreement the affected territories sent the information to the Imperial Institute of Entomology on forms, which although they varied slightly one from another had been designed to provide the information required in London. In 1958 standard forms (revised in the light of experience and supplemented by analogous forms for populations of locusts not showing gregarious behaviour) were accepted by the Food and Agriculture Organisation's (FAO) Technical Advisory Committee on the Desert Locust and were introduced by FAO throughout the desert locust distribution area. These reports are frequently supplemented by narrative accounts of campaigns in which some additional information on ecological conditions often appear.

ii. Early Studies on the Generalised Cycle of Breeding and Migration by the Desert Locust.

For the past thirty years each month's information has been plotted on a small scale (1:1M, 1:2M or 1:4M) map using symbols based on those designed at the First and Third International Anti-Locust Conferences. This series of maps has also been extended to include information collected from published and manuscript data which relate to the period before 1930. From these maps it has been possible to
Fig. 6. Relationship between seasonal breeding and rainfall regimes in Eastern Africa, (after Waloff 1946).
Fig. 7. Relationship between seasonal breeding and rainfall regimes in western and north-western Africa. (after Donnelly 1947).
Fig. 8. Relationship between seasonal breeding and rainfall regimes in north-eastern Africa and the Middle East, (after Davies 1952).
Fig. 9. Relationship between seasonal breeding and rainfall regimes in south-western Asia.

(after Porteiro and Poulton 1953)
delimit the total area subject to invasion and that, where breeding by the desert locust has been recorded (fig.5). From a more detailed study of these data the generalised cycle of breeding and migration was worked out.

In a series of Memoirs published by the Anti-Locust Research Centre (Waloff 1946, Donnelly 1947, Davies 1952, and Fortescue-Foulkes 1953) the details of these seasonal cycles and migrations were further analysed and their relationship with the climates were studied. In particular the relationship of breeding with the local rainfall regimes was summarised in a series of maps (figs.6-9). From the study of the presence of breeding in eastern Africa (Waloff ibid) during the three main rainy seasons, i.e. short rains (Oct.-Feb.), long rains (March-July) and monsoon rains (July-Oct.) it was concluded that:

"The breeding cycles in different parts of the area are closely connected with the rainfall regimes. It is realised that in addition to the primary determining factor, i.e. the presence of swarms, the occurrence of breeding in any area is determined not only by the incidence of the required amount of rainfall, but also by the suitability of soils and of temperatures. However, the closeness with which the breeding cycles over large parts of East Africa reflect the annual rainfall regimes suggest that in any area provided other conditions are suitable, the breeding cycle will largely depend on the seasonal distribution of rains."

The close connection between the seasonal distribution of rainfall and of desert locust breeding was also noted by Donnelly (ibid) for western and north-western Africa, Davies (ibid) for north-eastern Africa and the Middle East.
FIG. 10
SEASONAL BREEDING AREAS AND MAJOR MOVEMENTS
OF DESERT LOCUST SWARMS

Breeding areas in territories in which eggs or hoppers were recorded in 1938-1939.
- during January-June in 4-8 years.
- during January-June in 7-13 years.
- during July-December in 4-8 years.
- during July-December in 7-13 years.

Established or probable swarm movements.
from spring breeding areas.

Suspected swarm movements.
from spring breeding areas.
Breeding areas in territories in which eggs or hoppers were recorded in 1930-1953:
- during January-June in 4-6 years.
- during January-June in 7-13 years.
- during July-December in 4-6 years.
- during July-December in 7-13 years.

Main areas of October-December breeding.

Established or probable swarm movements:
- from summer breeding areas.
- from winter breeding areas.

Suspected swarm movements:
- from summer breeding areas.
- from winter breeding areas.
and Fortescue-Foulkes (ibid) for south-western Asia.

Although Waloff in her study (ibid) found in some cases that the limits of breeding coincided with the 1,000 mm. mean annual isohyet (see fig.6) she concluded that:

"The very wide range of annual rainfall under which breeding can occur indicates that the annual isohyets give no clue to the conditions under which it takes place, and that this must be studied by examining the actual records during each breeding season."

Donnelly (ibid) also found that in some areas the 50 and 500 mm. mean annual isohyets and the limits of breeding were coincident, and Fortescue-Foulkes (ibid) correlated the western limit of summer breeding with the 25 mm. June - October isohyet; but as neither they nor Davies (ibid) commented upon this conclusion I assume that they were in agreement with it.

The seasonal migrations of the desert locust between the often widely separated breeding areas in its distribution area have been summarised by Uvarov (1957). Figs. 10 and 11 show their generalised pattern.

iii. Frequency of Infestation by the Desert Locust.

These early studies showed the position of the breeding areas but gave no quantitative data on the relative importance of any area. The preparation of maps of the frequency of breeding by Miss Waloff et al (in preparation) constitute the first attempt of a quantitative estimate on the relative importance of the breeding areas. The first study of this kind aimed at finding the relative frequency
of infestation by swarms and by hopper bands throughout the
desert locust invasion area. The period chosen was 1938
to 1953 which includes 1 ½ plague and 1 ½ recession periods.
Also the percentage of infested years during this period
closely resembled that for a much longer period in both
Algeria and India and Pakistan. It was also felt that the
standard of reporting throughout the area over that period
was sufficiently uniform for comparisons to be attempted.
The degree square was adopted as the basic unit of comparison,
although they differ in area by some 30% between the equator
and 45°N the northernmost limit of infestation by swarms
during the study period. It was thought to be a unit of
such a size that most of the inaccuracies of reporting swarm
and hopper band positions would not be apparent in the final
presentation of the data, yet the differences of frequency
that exist over relatively small distances of a few hundred
kilometres, would not be disregarded. The solution evolved
to counteract the tendency for the relatively frequent
reporting of locusts in a well populated area, with the less
frequent reporting of a comparable infestation in a thinly
inhabited area, was to note only the presence or absence of
swarms and hopper bands during each month of the study period.
Thus the intensity of the infestation is not taken into
account; another reservation to be borne in mind is that
the infestations are neither uniformly nor randomly
distributed within a degree square and that this is likely
to be particularly so in areas of varied relief or where
Fig. 12. The distribution area of the desert locust during the period 1928 - 1953.
changes in soil and vegetation occur. However, this method of treatment enabled the vast amount of data available for this period to be presented in such a way that it is immediately apparent that some areas had been more frequently infested than others.

iv. Frequency of Breeding by the Desert Locust.

At the beginning of this study, data were available showing for each degree square the month during the 16 year period when breeding had occurred. The invasion area of the desert locust extended for approximately 29 million sq. km. (11 million sq. miles). During the years 1938-1953 breeding is known to have occurred in degree squares covering about half of this area (13 million sq. km./5 million sq. miles) see fig.12. The annual hopper frequency map was compiled by counting for each degree square the recorded presence of one or more hopper bands during each year of the 16 year period. The highest annual frequency thus recorded was 13/16 years in a degree square on the cost of the Sudan. Breeding was reported in 10 or more years (60% or more) of the period in 26 degree squares (approx. 2% of the total breeding area). These areas, which I will call high frequency breeding areas are to be found in the Nile Valley in the Sudan, along the coasts of the Red Sea and the Gulf of Aden, in south-eastern Ethiopia (the Ogaden) and in the desert areas along the Indo-Pakistan border. The areas of medium frequency ($\frac{5-9}{16}$ years or 30-60% of the time) are found not only surrounding the high frequency areas but also in north-western
Fig. 13. The annual frequency of breeding during the period 1938–1953.
Africa, and in parts of Arabia and the Middle East, and account for 28% of the breeding area. The remaining 70% of the area was infested in less than 30% of the years.

v. Definition of Major Breeding Areas.

The annual frequency map of breeding thus provided a basis for defining the major breeding areas (see fig. 13). For the purposes of this study the areas recording breeding in more than 60% of years will be termed high frequency breeding areas; those having breeding from 30 to 59% of the time will be called medium frequency breeding areas. These two groups will constitute the major desert locust breeding areas. The areas recording less than 30% of years with breeding will be known as low frequency breeding areas.

It was, however, already known that some areas have more than one breeding season during the year and it is possible, therefore, that some of the annual high frequency breeding totals within these areas are caused not by frequent breeding during each of the breeding seasons which occur in that area, but by less frequent breeding in each of the seasons occurring in different years. For this reason use of the monthly and quarterly frequencies will also have to be made.

vi. Rainfall Limits in Breeding Areas.

A close association between rainfall and breeding has already been noted. It is therefore conceivable that the high frequency areas experience rainfall conditions which are particularly suitable for breeding. It was already
<table>
<thead>
<tr>
<th>Year</th>
<th>Mean Annual Rainfall</th>
<th>No. of Rainfall Events</th>
<th>No. of Years</th>
<th>Mean Frequency</th>
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<td>1971</td>
<td>57</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1972</td>
<td>57</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1973</td>
<td>57</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1974</td>
<td>57</td>
<td>1</td>
<td>1</td>
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<tr>
<td>1975</td>
<td>57</td>
<td>1</td>
<td>1</td>
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<tr>
<td>1976</td>
<td>57</td>
<td>1</td>
<td>1</td>
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<tr>
<td>1977</td>
<td>57</td>
<td>1</td>
<td>1</td>
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<tr>
<td>1978</td>
<td>57</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1979</td>
<td>57</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1980</td>
<td>57</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1981</td>
<td>57</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1982</td>
<td>57</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1983</td>
<td>57</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1984</td>
<td>57</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

**Table 51**: Mean annual rainfall at the wettest and driest stations in areas of high and medium and low frequency of rainfall events.
known that certain mean annual isohyets delimit some of the breeding areas. Therefore a check was made to see whether or not mean annual isohyets delimit varying annual frequencies of breeding.

Mean annual rainfall figures were collected for the degree squares where breeding had been recorded and there were found to be rainfall stations in about 2/3 of them. An examination of these data shows that the desert locust has occasionally bred in areas where the mean annual rainfall is as low as 5 mm, or as high as 2,283 mm.

Within the high frequency breeding areas data were collected for 19 of the 26 degree squares. An interesting and possibly significant result was the similarity of the upper and lower limits of the rainfall range within 3 of these widely separated areas. In the Sudan, south-eastern Ethiopia and Indo-Pakistan the mean annual rainfall totals lay between 83-102 and 296-371 mm. (see Table 5). The other high frequency area is in Ethiopia and experiences a much wider range of mean annual rainfall (193-1316 mm.). Many of the stations recording the larger rainfall averages are high up on the Dessie Escarpment, outside the normal breeding area. It might be said, therefore, that the high frequency breeding areas of the desert locust are characterised by a mean annual rainfall of between 80 and 400 mm.

Areas other than these four high frequency breeding areas have a mean annual rainfall of between 80 and 400 mm.
The annual frequency of breeding during the period 1938-1953, showing the degree squares where all the rainfall stations recorded a mean annual rainfall of above 400 or below 80 mm.

high frequency
medium frequency
low frequency
mean annual rainfall at all stations in degree squares below 40 mm above 400 mm

breeding areas
Fig. 15. Annual frequency of breeding by the desert locust for the period 1938-1953 and mean annual rainfall within the breeding areas.

Inset. Rainfall variability.
These areas are shown in fig. 14 together with those receiving more or less than those amounts. These areas with rainfall similar to that of the high frequency breeding areas are to be found in parts of the spring breeding area which stretches from Morocco to Pakistan, in much of the summer breeding area of Africa and in the long and short rains breeding area of eastern Africa. Such breeding as has been recorded in these regions has been most frequent in the areas with a mean annual rainfall of between 80 and 400 mm. Fig, 15 shows that breeding seldom occurs in an area where the mean annual rainfall exceeds 1,000 mm. The two exceptions occur in parts of Uganda and Ethiopia which have two rainfall seasons, in one of which the mean does not exceed 750 mm, and in the other is between 750 and 1,250 mm; so that it is probable that breeding does not occur in areas where the average rainfall in any one season exceeds 1,000 or at most 1,250 mm. Breeding is also infrequent in areas where the mean annual rainfall is low, i.e. less than 80 mm. In view of the variability of rainfall (see fig. 15) in this area it would seem that conditions suitable for breeding do not occur very frequently in areas where the mean annual rainfall is below 80 mm, and above 500 mm, per annum.

vii. Forecasting of the Locust Situation.

From the knowledge of the seasonal patterns of the movements between the widely separated breeding areas and the position of the most frequently infested areas, it has been possible to forecast the general developments that are
likely to occur. These forecasts are circulated each month to all the territories in the distribution area of the desert locust.

Initially these forecasts were based only on a knowledge of analogous past situations. The more recent work of Aspliden and Rainey (in preparation) has established that the major movements of desert locust swarms do in fact take place down-wind, towards and with zones of convergent wind flow. They feel that this accounts for the close and apparently purposeful association between the distribution of rainfall, which is essential for breeding, and the arrival of swarms in these areas where they subsequently breed. This work has also enabled indications of the onset of such movements to be recognised. These findings have led to improvements in short-term forecasts.

This study was started to learn more about the association between rainfall and breeding, and the limiting conditions of moisture in which breeding takes place. In this way it was hoped that data currently available on recent rainfall could be used to improve the interpretation and forecasting of events in the desert locust breeding areas.

viii. Relationship between Weather and Breeding.

The relationship between weather and breeding falls into three phases:

1: factors affecting maturation.
2: factors affecting oviposition.
3: factors affecting the successful development of the eggs.

Rainfall has been noted by many workers such as Norris (1957), Popov (1958) and Rao (1960) as playing an important part in 2 and 3, and it also appears (Maxwell-Darling 1934, Hamilton 1950, Norris 1957 and Rao 1960) to be involved in an as yet unexplained way in 1.

A preliminary study (see Page 31) had shown that the major desert locust breeding areas experience a similar mean annual rainfall. It was thus decided to study further the rainfall conditions accompanying breeding in one well documented major breeding area. In particular the association between rainfall and the formation of soil moisture conditions suitable for oviposition were studied and the limiting conditions of rainfall under which breeding takes place were sought. These factors were also studied with reference to the monthly rainfall data which are available at the time when the interpretation and forecasting of events in the desert locust breeding areas are being made. For at the beginning of each month when this is being done the meteorological services of this and other areas broadcast Climat Messages which include the previous months rainfall total.

ix. Selection of a Major Breeding Area for Study.

I began by selecting an area where there is only one major rainy season which occurs at a time when the temperature conditions are unlikely to be unsuitable for
The frequency of breeding during July - September showing the average position of the ITCZ in July.
brooding. This is likely to be true of the areas of summer rains in Africa and south-west Asia.

The quarterly frequency map for July-September (fig. 16) gives a good indication of the frequency of breeding at this season which takes place in association with these rains; it also shows the end of the previous seasons breeding which takes place in the spring in north-west Africa and the Middle East and in association with the long rains breeding on the Somali Peninsula. From this map it can be seen that the Indo-Pakistan and Sudan-Ethiopian areas are major breeding areas at this season. It also shows how the main areas of breeding at this season lie between the average surface position of the ITCZ in July and the area of maximum rainfall which occurs at the southernmost extension of the overlying easterly winds. The ITCZ along which the swarms are to be found at this season, oscillates both north and south of this position. However, it would appear that it is in between the average position of the surface ITCZ and the zone of maximum rainfall that the swarms most frequently find conditions suitable for breeding.

From the point of view of meteorological data and of length of recorded locust history the Indo-Pakistan area is much the better documented one. It is also an area where the monsoon breeding takes place in a region of relatively uniform relief and where there is little surface drainage. Thus this is a particularly suitable area in which to study the association of rainfall and breeding as
the complicating factor of moisture entering or leaving the area as run-off is reduced to a minimum. Also as Rao (1960) states:-

"In north-west India the general atmospheric temperatures are usually not adverse to locust activity except in the winter months."

His findings on summer breeding in this area can be summarised as follows:--

1) Soaking rains are required to provide the requisite conditions of soil temperature and moisture.

2) Sandy or loamy soils must be available to ensure the necessary drainage, but that even these might become waterlogged after very heavy rain, thus prejudicing the chances of survival of any eggs present. On the timing of the rainfall he states:--

"Good rainfall in June and July would result in an early development of swarms, which may lead to the development of a second summer generation, if further good rains should happen to fall in August or September. On the other hand, a long break in August would bar further breeding, even if there should be the requisite amount of precipitation in September. Heavy rainfall in August or September would generally result in the development of late breeding and consequently lead to a considerable over wintering of swarms in the Punjab, United Provinces and Sind (Rao ibid).

It has long been accepted that the varying quantities of rain received during each year play an important part in the distribution and the success or failure of the monsoon breeding in Indo-Pakistan. References in the literature are numerous on the point. Rao (ibid) whilst acknowledging the drawbacks of using monthly rainfall totals
to gauge the affect rainfall has on breeding, nevertheless concluded,

"On the whole, however, the monthly totals have proved for all practical purposes quite useful for purposes of correlation."

In his and Pruthi's (1951 etc.) publications the monthly rainfall totals for selected stations are listed. Within their texts qualitative assessments of the abundance or scarcity of precipitation during a particular season are given, together with the resultant effect on locust breeding. However, no attempt is made to relate the rainfall totals to a quantitative standard such as the mean monthly rainfall for these stations. It is often assumed that greater than average rainfall causes exceptionally suitable conditions for breeding, although it has been suggested (Rainey verbal communication) that the reverse might hold in the wetter areas where breeding occasionally takes place.

x. Proposed Investigations.

In view of these facts it was felt worthwhile in this study to compare the actual amounts of monthly rainfall with the mean to see what effect departure from this mean has on the breeding of the desert locust during the summer in India and Pakistan. The results of this study appear in chapter 3. Other more detailed studies of the association of daily rainfall and the recorded locust events such as maturation and egg-laying have been made as well as studies of the cumulative total of rainfall received before laying
in an attempt to throw further light on the limiting conditions of rainfall under which breeding takes place in this area.

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CHAPTER I

SOIL MOISTURE AND OVIPOSITION

Before the significance of the rainfall data can be estimated some assessment of the moisture conditions under which oviposition takes place and the effect of rainfall on soil moisture has to be made.

i. Classification of Oviposition Behaviour according to Moisture Conditions.

Popov (1958) found that he was able to make a rough classification of oviposition behaviour and distribution from the moisture level in the soil. He found that on the 14 occasions in East Africa where he had studied oviposition in progress during or up to a fortnight after rainfall, the resultant egg-fields could be divided into three groups according to the depth of moisture below the surface.

I. Under Humid Conditions: where the moisture level, i.e. the level beneath which the soil was visibly moist, was about 0.5-2.0 cm. below the surface, which occurred in these instances about 48 hours after rainfall.

II. Under Moderately Moist Conditions: when the moisture level was from 2.5-6.5 cm. below the surface some 4-5 days after the rain.

III. Under Dry Conditions: when the moisture level was more than 7.5 cm. below the soil surface which occurred more than a week after rain.
ii. **Selection of Egg-Sites.**

The selection of the egg-sites by the settled locust swarms under these three sets of conditions varied considerably. Both under humid and under dry conditions the choice of sites was highly selective, so that during the initial period of probing and digging in search for suitable oviposition sites which took place many of the bore holes made were rejected indicating that much of the area was found unsuitable for oviposition. In the first case the locusts which had been basking, remained on and utilised these warmer slopes, and in the third only the most humid areas were selected (see pp.2 et seq.) In this case the limited number of suitable sites led to very dense groups of egg-pods being laid in them.

The intermediate case of moderately moist areas the depth of moisture seemed to be acceptable, and laying proceeded with few of the bore holes being rejected. Sometimes oviposition occurred more than once at the same site. When this happened and the moisture conditions at the time of both layings differed, then the position of the egg-pods varied according to the pattern noted above; however, if the soil moisture conditions were similar on both occasions then no obvious difference in the choice of egg-sites was noted.

iii. **Laboratory Experiments of Moisture Requirements during Oviposition.**

To assist in interpreting these and other observations
TABLE 6

Frequency of digging (D) and laying (P) in tubes containing moist sand at different depths under dry sand (after Popov 1958)

<table>
<thead>
<tr>
<th>Thickness of dry upper layer (cm.)</th>
<th>Thickness of moist lower layer (cm.)</th>
<th>Date (January):</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>10</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D P</td>
</tr>
<tr>
<td>1</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>4</td>
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<td>0</td>
</tr>
<tr>
<td>10</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>6</td>
</tr>
</tbody>
</table>
TABLE 6 (continued)

Frequency of digging (D) and laying (P) in tubes containing moist sand at different depths under dry sand (after Popov 1958)

<table>
<thead>
<tr>
<th>Date (January):</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>14</td>
<td>15</td>
</tr>
<tr>
<td>0 1</td>
<td>1</td>
</tr>
<tr>
<td>0 3</td>
<td>2</td>
</tr>
<tr>
<td>0 0</td>
<td>0</td>
</tr>
<tr>
<td>1 0</td>
<td>1</td>
</tr>
<tr>
<td>1 2</td>
<td>1</td>
</tr>
<tr>
<td>0 0</td>
<td>1</td>
</tr>
<tr>
<td>0 0</td>
<td>0</td>
</tr>
<tr>
<td>0 0</td>
<td>0</td>
</tr>
<tr>
<td>2 6</td>
<td>9</td>
</tr>
</tbody>
</table>
he had made on oviposition in the field, Popov (ibid) carried out some laboratory experiments to study the effects of the moisture conditions under which oviposition takes place.

iv. Depth of Moist Sand Required for Oviposition.

It was found (see Tables 6 and 7) that oviposition never occurred in completely dry sand, although there was much abortive probing and digging under these conditions. Normal oviposition only took place when the whole egg-pod could be laid in water-moistened soil. For this condition to be satisfied the moist layer had to be at least 6 cm. deep. Eggs could, however, be successfully laid into moist sand which was overlain by as much as 8 cm. of dry sand. These were limiting but not optimum conditions for oviposition in this type of tube, for where a larger horizontal area is available pods have been placed in a layer as small as 3 cm. in depth (Norris unpublished).

v. Effect of Simulation of Varying Amounts of Rainfall on Oviposition in the Laboratory.

Popov (ibid) attempted to produce in the laboratory the soil conditions caused by varying amounts of rainfall. These experiments were carried out in a constant temperature room where the general temperature was maintained at 28°C. The tubes of moistened sand were in a position where in the daytime, when extra heat and light were supplied by a 60 watt electric lamp, the temperature rose to about 32°C.
### TABLE 7

Quantitative tests of soil moisture preference
(after Popov 1958)

<table>
<thead>
<tr>
<th>Amount of water added (mm.)</th>
<th>Number of tubes</th>
<th>Thickness of dry surface layer (mm.)</th>
<th>Depth of penetration of moisture (mm.)</th>
<th>Depth of pod (mm.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>2</td>
<td>Sand dry throughout</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>7.5</td>
<td>5</td>
<td>11 (8-15)</td>
<td>54 (45-65)</td>
<td>-</td>
</tr>
<tr>
<td>10</td>
<td>12</td>
<td>7 (4-15)</td>
<td>75 (45-90)</td>
<td>80 (75-85)</td>
</tr>
<tr>
<td>15</td>
<td>11</td>
<td>5.5 (0-12)</td>
<td>123 (90-150)</td>
<td>82.5 (65-100)</td>
</tr>
<tr>
<td>20</td>
<td>9</td>
<td>6 (0-12)</td>
<td>180 (145-200)</td>
<td>85 (60-110)</td>
</tr>
<tr>
<td>30</td>
<td>3</td>
<td>5 (0-10)</td>
<td>200 200+</td>
<td>85</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>48-hour tubes</th>
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<tbody>
<tr>
<td>5</td>
</tr>
<tr>
<td>7.5</td>
</tr>
<tr>
<td>10</td>
</tr>
<tr>
<td>15</td>
</tr>
<tr>
<td>20</td>
</tr>
<tr>
<td>30</td>
</tr>
</tbody>
</table>
### TABLE 7 (continued)

Quantitative tests of soil moisture preference (after Popov 1958)

<table>
<thead>
<tr>
<th>No. of tubes showing probing</th>
<th>Total</th>
<th>Mean</th>
<th>No. of tubes with pods</th>
<th>Total</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Probings</td>
<td>Pods</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>?</td>
<td>?</td>
<td>Nil</td>
<td>Nil</td>
<td>Nil</td>
</tr>
<tr>
<td>4+</td>
<td>22+</td>
<td>5.5</td>
<td>Nil</td>
<td>Nil</td>
<td>Nil</td>
</tr>
<tr>
<td>12</td>
<td>49</td>
<td>4.1</td>
<td>5</td>
<td>10</td>
<td>0.8</td>
</tr>
<tr>
<td>10</td>
<td>20+</td>
<td>2.2</td>
<td>8</td>
<td>12</td>
<td>1.1</td>
</tr>
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<td>7+</td>
<td>20+</td>
<td>2.6</td>
<td>6</td>
<td>10</td>
<td>1.1</td>
</tr>
<tr>
<td>3</td>
<td>7</td>
<td>2.3</td>
<td>1</td>
<td>2</td>
<td>0.7</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>No. of tubes showing probing</th>
<th>Total</th>
<th>Mean</th>
<th>No. of tubes with pods</th>
<th>Total</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>?</td>
<td>?</td>
<td>Nil</td>
<td>Nil</td>
<td>Nil</td>
</tr>
<tr>
<td>4</td>
<td>?</td>
<td>?</td>
<td>Nil</td>
<td>Nil</td>
<td>Nil</td>
</tr>
<tr>
<td>10</td>
<td>31+</td>
<td>4.0</td>
<td>3</td>
<td>5</td>
<td>0.5</td>
</tr>
<tr>
<td>10</td>
<td>40</td>
<td>4.0</td>
<td>8</td>
<td>16</td>
<td>1.6</td>
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<td>33</td>
<td>3.7</td>
<td>8</td>
<td>14</td>
<td>1.6</td>
</tr>
<tr>
<td>2</td>
<td>9</td>
<td>4.5</td>
<td>2</td>
<td>3</td>
<td>1.5</td>
</tr>
</tbody>
</table>
The sand used had been sifted through a sieve of 1.5 mm. mesh, and was placed in tubes 20 cm. long which had a slit in the bottom to allow drainage to take place. The water was poured onto the surface of the sand and was allowed to seep into it naturally. The results of these experiments are shown in Table 7. The range and the average depth to which the various amounts of water penetrated after 24 and 48 hours are shown in the table as is the thickness of the dry layer which had formed at the top of the tubes during the same periods of time. The average penetration varied from 7-9.5 + times the depth of added water. When 10 or more millimetres of water were added in no case did the depth of the dry layer exceed 3 cm., i.e. half the maximum depth which had been penetrated in the laboratory experiments. The depth of moist sand beneath this dry layer into which the eggs were placed varied between 4.5 and 20 cm. when 10 or more millimetres of water were added, a depth of moist sand again comparable with his earlier results.

It was found that 24 hours after simulating a fall of 5 mm. the sand appeared to be dry. In this case and also when 7.5 mm. were added no laying took place.

vi. **Amounts of Simulated Rainfall Found Suitable for Oviposition.**

Moisture conditions representing a fall of 10 mm. were sometimes adequate for laying, particularly within the first 24 hours. The conditions most suitable for
Fig. 17. Calculated effect of intensity of precipitation on conservation of moisture from 1 inch of rain. (after Hopkins, 1940)
oviposition after both 24 and 48 hours, were those caused by water representing falls of 15 and 20 mm; when conditions representing 30 mm were made they appeared to be too moist during the first 24 hours, but subsequently became acceptable. These records support Popov's earlier work on the requisite depth of soil moisture and also agree closely with the conclusion that Rao (1960) made after 9 years of extensive field research and studies of the available locust data for India prior to 1940 and the relevant meteorological records.

"It is only when a heavy fall of over an inch [25 mm.] of rain occurs that sandy soils become sufficiently wet to allow of eggs being laid by parent locusts. If instead of one drizzling rain falling on one particular day, the same amount of rain is spread over 3 or 4 days, the effect would not be the same, as the moisture would not then penetrate sufficiently deep into the soil."


Some results based on observations for 1922-1938 on this latter point of Rao's are given by Hopkins (1940) who, noting the increased proportion of soil moisture retained in a fallow soil in Saskatchewan, Canada after heavy rainfall (fig.17) assumed that this was caused by the deeper penetration of moisture, after such falls of rain, reaching a zone where evaporation is less effective. These results apply to an area where it has been estimated that in the absence of precipitation 6 mm. of moisture

1This soil had been placed in water-tight tanks set in pits at the Soil Research Station, Swift Current, Saskatchewan, Canada
Fig. 18. Calculated net conservation of moisture by soil, 10 days after occurrence of various one-day amounts of precipitation. (after Hopkins 1940)

Fig. 19. Calculated percentage conservation by soil, 10 days after occurrence of various amounts of precipitation in excess of the one-day "effective minimum" (after Hopkins 1940)
would be lost from the soil in May and June and 8 mm. in July and August. Comparable figures for India are not available but the total water loss by evaporation at Pusa, India for the 7 month dry period has been calculated as not exceeding 50 mm. Russell (1958) found that the loss of water from bare soil at Rothamsted, England did not differ very greatly from that lost from bare soils at Poona and Pusa in India. At Rothamsted following rainfall in the summer 13 mm. of moisture is evaporated in the first 5 days after which the rate of evaporation falls rapidly from about 2.5 mm. a day to 2-1.3 mm. a week. So that after a drought of 6 weeks about 25 mm. of moisture has been lost and during the 3 months drought from June - August 1921 the total loss was only 33 mm. When precipitation occurs the amount of evaporation increases. Fig.18 shows the amount of moisture estimated to be conserved in the soil at Swift Current, Saskatchewan 10 days after varying amounts of rain have fallen. It shows that 9 mm. in May and June and 12 mm. in July and August are required to offset the evaporation of the following 10 days. This latter amount is comparable to the amount lost at Rothamsted in the 10 days following rain during the summer. These amounts can be regarded as the 'minimum effective' rainfall for the area. Fig.19 shows the percentage moisture conserved 10 days after precipitation exceeding these amounts has fallen, and again indicates the increased
efficiency of heavy falls of rain.

viii. The Availability of Soil Moisture.

The inter-relating factors (which will be presented in greater detail below) affecting the quantity of soil moisture available for the eggs, include not only the quantity of the precipitation and the intensity with which it fell but also other climatic factors such as temperature, humidity and wind-speed, all of which help to determine the rate of evaporation of moisture from the soil surface. So too does the nature of the soil play an important part in regulating the availability of water.

Most of the published data on these subjects are based on evidence from temperate latitudes, and much of the quantitative evidence used in papers on the water-balance in arid and semi-arid zones are also from these sources. However, as Russell found that water losses from the bare soil at Rothamsted and in arid and semi-arid zones did not differ widely, it may be permissible to use these data until actual values from the areas being studied are available.

ix. Water Balance in the Soil.

When rainfall reaches the soil surface part of it infiltrates into the soil where some of it becomes available for making conditions suitable for oviposition, whilst the rest of it is lost for this purpose by run-off, evapo-transpiration and drainage into the lower layers which cannot be utilised by the locusts.
Heatt and Schloemer (1955) gave the relationship of these factors as:

\[ dQ = P - r - q - E. \]

Where \( dQ \) = changes in moisture in the zone being studied,
\( P \) = precipitation,
\( r \) = run-off,
\( q \) = drainage into the lower layers,
\( E \) = evapo-transpiration.

Burgos and Tschapek (1958) took more factors into consideration and described the relationship as follows:

\[ Q'' = Q' + \text{sum of incoming moisture} - \text{sum of outgoing moisture} \]

where \( Q' \) = initial moisture content of the soil,
\( Q'' \) = final moisture content of the soil,
\( \sum \text{incoming moisture} = Pr + Co + Co + Ca \) Burgos and Tschapek,
\( \sum \text{outgoing moisture} = Ev + Rf + Ev + F \) after Albrecht.

where \( Pr \) = precipitation,
\( Co \) = condensation of atmospheric water vapour in the soil due to differences in tension between the vapour in the atmosphere and that in the soil,
\( Co \) = condensation of vapour from lower horizons in the upper horizons due to the same factor,
\( Ca \) = capillary movement of water from lower to upper horizons,
\( Ev \) = evapo-transpiration,
\( Rf \) = surface run-off,
\( Ev \) = evaporation in the soil i.e. movement of vapour from upper to lower horizons,
\( F \) = loss of water in upper horizons by infiltration.

\( Rf + F \) can be written as \( R \) the total run-off (surface and internal).

In soils where the water table is at depths greater than 3 or 4 metres (which is so in much of the Desert Locust breeding areas) Ca is of very limited importance. For many soils Co, Co and Ev are also of little importance, and although opinions of their importance in semi-arid soils vary, Albrecht, like Heatt and Schloemer, felt able
Fig. 20. The range of minimum infiltration rates with row crops on wet soils.
(after Musgrave, 1955)
to express the water balance adequately without the use of these factors. Thus the relationship becomes

\[ Q_1 = (Q_0 + Pr) - (Ev + R) \]

which is essentially the same as that used by Heatt and Schloemer.

x. **Incoming Moisture.**

a) **Rate of Infiltration.**

As the rainfall reaches the soil surface its rate of infiltration is determined by the permeability of the layers of the soil, and is greater in sandy soils than in those with a higher proportion of clay particles. Where there are few clay particles the initial rate of infiltration can be over 50 mm./hour where the soil is well cultivated, but any degree of compaction reduces this rate greatly. Musgrave (1955) gives minimum rates of infiltration for the main soil groups (Fig. 20).

Other factors which affect infiltration are the season of the year and the temperature of the soil and water. For sand, the minimum rate given is 8-11 mm./hour\(^{-1}\). Milthorpe (1960) in a research review, states that for many purposes it may be assumed that infiltration rates are never greater than 15 mm./hour\(^{-1}\) and that when showers are of low intensity all the water enters the soil. Dubief (1955) summarises the laboratory and field data on the effect of precipitation on soil moisture in the Sahara, an area where breeding by the desert locust occasionally takes place. In the samples of sand studied, the pore
space occupied between 25 and 30% of the dry soil; the infiltration rates varied greatly (0.02-3.0 mm./sec.) but these were nearly always faster than the intensity of rainfall which seldom exceeds 0.03 mm./sec. This is of importance in minimising the amount of run-off, which occurs when there is an excess of rain falling over the rate of infiltration. In arid and semi-arid zones, where the average run-off for an entire drainage basin is considered over a period of several years, the quantity is found to be small, although during that time large amounts may have occurred locally.

Schoeller (1959) suggests that where the annual precipitation is less than 200 mm. run-off may be of two types. The rainfall amounts which are generally small normally fall on unsaturated soil. However, there is usually some surface flow during the year in some stream beds which means that either the soil must have become saturated in a limited area, or that the intensity of the rain must have been greater than the rate of infiltration. Dubief (ibid) maintains that surface flow will occur in the Central Sahara when a fall of rain with an intensity of 5 mm./minute exceeds 5 mm.

b) Soil Capacity.

When all the pores in the upper part of the soil are filled with moisture, the soil is said to be saturated with respect to water and is at its maximum retentive capacity. If no further rain falls, drainage by fairly
Fig. 21. Relationship of various forms of soil moisture to higher plants.
(after Buckman & Brady, 1960)
rapid percolation of water into the lower layers continues and the larger pore spaces are emptied. At this stage the soil is at its field capacity. Moisture movement continues by capillary forces, is much slower and can continue until only the moisture associated with the surfaces of the soil particles remains. This moisture can only move as vapour and the moisture content of a soil in this condition is known as the hygroscopic coefficient. The wilting point or coefficient is the lowest moisture content of the soil at which water is available to plants.

c) Depth of Penetration by Moisture.

Field observations at Tamanrasset, Sahara, reported by Dubief (ibid) showed that the depth of sand moistened was some 10 times as great as the amount of rainfall that had been recorded. Other observations at Tindouf in Mauritania suggested a similar relationship. He concluded that the rainfall would infiltrate quickly into sandy soil reaching a depth at least 10 times as great as the measured precipitation and that this layer would eventually retain about 3-6% moisture. After the cessation of the rainfall, the water would continue to percolate downwards, but at a very reduced rate of about 2 mm./day. Summarising the knowledge of the water content of the sand-dunes in the Sahara, he says that a single fall of a 100 mm. (a maximum value not exceeded even in a rainy period) would moisten a layer of not more than 1.5 to 2 metres deep. He also states that to moisten the
surface layer (about 80 cm, deep through which moisture moves by capillary forces) 60 mm. of rain is needed after a long dry period, again an amount seldom recorded as a single fall in the Sahara. These assumptions he finds are confirmed by the observations reported by Cauvet (1908) that the layer below 2.5 metres is always dry.

d) Effect of Plants on Moisture Penetration.

Glover P.E. (1950) and Glover J. (1962) studied the depth of moisture penetration within differing vegetation complexes in Kenya and the Somali Republic (N. Region.). Certain of their observations on plant roots in this area had suggested that there might be a relationship between the top cover, the root growth form of plants and the visible penetration depths of rain water into the soil. This was done by measuring the depth of visible moisture penetration along the walls of trenches dug after a known quantity of rain had fallen, or water had been added to, an area. They found that the greater part of the rainfall had penetrated into the soil 2 hours after the rain and that there was only slightly more penetration during the next 12 hours. The experiments showed that many factors modified the penetration of the moisture. These included the slope of the ground and the relationship of the trench to that slope, the presence of gravel beds in the soil and the vegetation pattern. However, where the trenches were associated with bare ground the depth of penetration was approximately 10 times greater than the amount of rain
which had fallen. Where there was a plant cover greater penetration of moisture occurred beneath the plants and it occasionally amounted to 60 times the rainfall. In Kenya for the communities and soil types and the amount of rainfall studied the depth of rain-water penetration was approximately equal to the height of the plant plus the normal penetration the shower would have made into a bare soil. The sectional area of the wet soil beneath each clump of vegetation was also found to be approximately equal to the sectional area of the clump showing above ground plus an area corresponding to the amount which would have been moistened had there been no plant cover.

e) Moisture Content of the Soil in the Rajasthan Desert, India.

Some data affecting the water balance in the soil of the study area are available and can be found in the Proceedings of the Symposium on the Rajputana Desert, September 1952. Raychaudhuri summarises the nature of the moisture content at 6 experimental stations run by the Indian Council of Agricultural Research. The sandy soils can hold up to 14% moisture, but in the hot season the moisture in the surface layers is reduced to 3-4%. A fall of rain of 25 mm. in this area is said to penetrate to a depth of 150–200 cm. an amount slightly less than that quoted by Dubief for the Sahara, but again moistening the soil to a depth much greater than the minimum requirements (3-5 cm.) for oviposition under laboratory
Fig. 22. The general relationship between soil moisture characteristics and soil texture. (after Buckman & Brady, 1960)
conditions by the desert locust.

The fate of this moisture during a subsequent dry period may indicate why the moisture conditions created by a fall of 25 mm have been observed to be the minimum acceptable under field conditions in India.

f) Availability of Moisture.

Fig. 22 shows the moisture conditions characteristic of various soil types and indicates the amount of water available for evapo-transpiration or absorption by the locust eggs.

g) Availability of Soil Moisture to Locust Eggs.

It is not known if the eggs of the desert locust are able to utilise the moisture from a soil below the wilting coefficient. The experiments of Husain, Ahmad and Mathur (1941) suggest that in sandy soils it is only the hygroscopic moisture that is not available for absorption by the eggs (see p.8). Clark (1947) in a study on the Australian plague locust (Chortoicetes terminifera Walk.) also said that it was thought that hygroscopic moisture is not available to the eggs of locusts. Studies on other insects in Australia such as the cockchafer (Aphodius howitti) have shown that they react to the force with which the water is held in the soil and not to the absolute amount of water present. For this insect water held at pF's between 2.5 and 3.75, i.e. when the soil is between its field capacity and wilting point (see fig. 21) was utilised by the cockchafer's eggs, but where the pF
was 4.0, i.e. approaching the wilting point, the eggs lost water to the soil and so died, Andrewartha (1958).
It is most probable that locust eggs have a similar reaction to water in the soil.

xi. Outgoing Moisture.

a) Evaporation.

Water is lost from the surface of soil which is saturated, at approximately the same rate as from an open water surface, but when the surface dries out, the rate of evaporation decreases markedly. Milthorpe (1960) quotes various authors, including Penman, working at Rothamsted where clay and sandy loams are present, as stating that very little further evaporation occurs from soil after 16-25 mm. have been lost. This amount of moisture is equivalent to that available in the top 10-15 cm. of soil. He also quotes Staple and Lehane who, working in Saskatchewan with loam soil, found that 20 mm. was lost fairly rapidly from a wet soil, after which a further 7-8 mm. was lost slowly if there was a prolonged period without rain. However, it should be noted that in neither of these instances was a sandy soil being studied, and as can be seen from fig. 22, less moisture would have been available for evaporation from a sandy soil.

The initial rate of evaporation influences the amount of moisture which is lost; with a low rate of evaporation of about 2.5 mm./day evaporation is rapid
Fig. 23. The drying rates of four soils under uniform conditions of temperature, vapour pressure and wind speed in a tunnel. (Milthorpe, 1960)
until some 20-25 m.m. have been lost, but with a faster initial rate of evaporation of some 5-6 mm./day (7 mm./day has been estimated for Rajasthan, see page 65) the dry layer is formed after only 8-10 mm. have been lost. The water loss at the slower rate is almost entirely due to further downward flow.

Fig. 23 illustrates these points showing the sierozem losing less moisture at the high rate of evaporation than the other soils for which the initial rate of evaporation was lower. The change in evaporation rates is shown clearly.

Milthorpe concluded from these and other studies that:

"Depending on the rate of potential evaporation, the degree of cover and time from re-wetting, as much as 10 to 30 mm. representing the available water in the top 10-18 cm. of soil may be lost via the soil surface for each cycle of wetting."

This amount may be increased when there is a cover of vegetation, for then the dry layer which inhibits evaporation takes longer to form.

b) Evaporation in India.

Raman and Satakapan (1935) used the following modified form of Rowher's empirical formula for calculating mean monthly evaporation rates in India:

\[
E = (1.465-0.018B)(0.44+0.118w)(100-1)e
\]

where:
- \( E \) = mean daily evaporation from the U.S.A. standard type evaporimeter.
- \( B \) = barometric pressure in inches of mercury.
- \( w \) = mean wind velocity in miles per hour.
- \( h \) = mean relative humidity for the period.
- \( e \) = mean vapour pressure of the period in inches of mercury.
TABLE 8: Mean monthly and annual evaporation in inches (after Pramanik 1952).

<table>
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<tr>
<th>Station</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>Aug</th>
<th>Sept</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
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<td>23.3</td>
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<td>23.6</td>
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Values for several stations in the desert locust breeding areas of India and Pakistan were given in the Proceedings of the Symposium on the Rajputana Desert by Pramanik (1952) (see Table 8). The values for Bikaner, Jodhpur, Jaipur, Deesa, Hyderabad and Jacobabad were re-calculated by Pramanik using more recent meteorological data than that available to Raman and Satakopan. Very few measurements of evaporation have been made in the Rajputana Desert. Some were made by Fergusson (1944) for the years 1932-1937 of evaporation from floating pans in Kailana and Bussamund Reservoirs and from shore pans 30.5 metres from these reservoirs at Jodhpur. The mean annual evaporation from the floating pans was 2600 mm. and from the shore pans 2900 mm. When the evaporation at Jodhpur was calculated using the formula and the meteorological data for these years, the result obtained was 4600 mm. Pramanik, allowing for a greater rate of evaporation amounting to 3200 mm./annum, had the pans been situated further away from the water, has estimated that to obtain values of evaporation from this formula the results should be reduced by a factor of 2/3.

c) Estimated Water Loss from Soil Surface in Rajasthan.

Ramdas (1952) at the same symposium discussed evaporation in this area. He used the following method to obtain an estimate of the loss of water from the soil surface in Rajasthan.

The modified formula of Rowher indicates the power
of evaporation of the layer of air one foot above the soil surface. Experiments at Poona with the U.S.A. standard type evaporating pans, one set at standard exposure and the other set flush with the soil surface, had shown the following relationship between E-evaporation one foot above the surface and E₀-evaporation at the soil surface.

$$E_0 = 0.845E.$$  

Further experiments had shown that when a ring of wet soil surrounded the pan set flush with the soil, the rate of evaporation decreased but that, as the diameter of the wet soil increased, a limiting value of $$E_{or} = 0.7E_0$$ was soon reached. In a rainy season the value of $$E_0$$ will be approximately the same as $$E_{or}$$ but this is not so in a dry season, when the surface soil is dry. Thus, Ramdas multiplied the values obtained from the standard U.S. type evaporimeters by both these reduction factors.

Thus $$E_{or} = E \times 0.845 \times 0.70 \approx 0.6E.$$  

Ramdas applied this relationship to West Rajasthan, assuming there to be no cover of vegetation and a dry soil for most of the year. Taking the pan evaporation to be 2500 mm. for a year, he obtained a value of 1500 mm. for evaporation from a lake or a large expanse of wet soil. A further correction was then made to allow for the soil being dry for much of the time, which would mean an annual total of less than 1500 mm.
Experiments had been carried out at Poona to find the relationship between evaporation $E_0$ when the soil surface is moist and $E_z$ when the depth of the water-table is $z$ cm. below the surface. The following relationship was found:

$$E_z = E_0 \times 10^{-a \cdot z}$$

where $a$ is a constant depending on the soil type.

For the sandy soils of Rajputana, Ramdas used the value 0.008 for $a$ and assumed the water-table to be at a depth of 100 cm. (Ramdas 1948). He obtained a value of 240 mm./annum, that is the evaporation almost equals the mean annual rainfall of the area. Thus one can assume that, except for short periods during the rainy season, there will be a moisture deficit in the soil.

xii. Conclusions.

It can be seen that to obtain reliable estimates of the soil moisture conditions under which oviposition has taken place - for direct measurements are seldom available - a great deal of information on soil type and structure, climate and detailed reports of locust behaviour must be known. As can also be seen from the previous section, these factors are intricately interwoven, and are further complicated by the fact that the soil in these areas is seldom saturated so that the percentage loss of moisture following equal amounts of precipitation may vary considerably.

The data available, even for the better documented
areas are limited. In the Rajasthan Desert area of India, daily rainfall data are available but there are few data on evaporation. This, together with the fact that detailed information on the egg-sites is not available, makes it improbable that any but the most general observations on the soil moisture conditions, under which oviposition occurs, can be made, except during field experiments when they can be measured.

However, it is known that desert locusts prefer to lay their eggs in a soil which has a dry surface layer. This means that the eggs will normally be laid in a soil where the rate of evaporation has already fallen to a low level. Values of daily evaporation for the Rajasthan area, calculated from the monthly values available\(^1\) suggest that an evaporating power of about 7 mm./day is a reasonable one for the area during the wet summer months. In this case it may be assumed from the values quoted by Milthorpe that the dry surface layer will have been formed after only some 8-10 mm. of moisture have been lost, i.e. about half the water available in the top 10-15 cm. of soil. If this is so, it can be seen from the diagram on the relationship between soil moisture characteristics and soil texture (fig.22) that even in the coarsest sand about 3% water is present when half the available moisture has been removed. Laboratory work

\(^1\) average evaporation for the 3 months July-September is 600 mm. which gives an average daily value of approximately 7 mm. Pramanik (1952)
by Hunter-Jones (in preparation) has shown that oviposition takes place readily in the laboratory under such moisture conditions and that a normal hatch results when the tubes (covered with a metal cap to reduce evaporation) containing the eggs are incubated at a temperature of 28°C. The range of moisture from which hatching resulted was from approaching 25% when the soil was nearly water-logged falling to 1%. The value of 3% moisture beneath the dry layer also agrees with the value of 3-4% moisture quoted by Raychaudhuri (1952) (see page 58) for the value of moisture of the surface layers during the hot season in Rajasthan. Providing that maturation of the population has occurred, once the soil surface layer has been moistened to a depth of some 6 cm. laying could take place. This depth of soil could be moistened by a fall of rain of about 6 mm. It is apparent though, from the estimates of the evaporative power of the air, also from Popov's laboratory experiments, that this amount of rain would be removed very rapidly from the soil. Unfortunately he does not give the amounts of rain which had fallen before his observations were made, but his classification suggests that the depth of the dry surface layer may increase fairly constantly with the passage of time. Any further moisture falling in this type of area penetrates quickly to a greater depth, seldom lying on the surface, so that under the conditions of rapid evaporation which are present, the top surface
would again become dry in a day or two.

The fact that the locusts can delay oviposition for up to 72 hours and that they show a preference for laying through a dry surface layer, would mean that they would normally be able to wait until these conditions had become established. This in turn would minimise the chance of the eggs becoming dessicated as the soil dries, a phenomenon not unknown under field conditions (Brown E.S. 1947). His observations suggest that these eggs had been laid under conditions of high moisture as the dessicated eggs had been laid on the higher better drained areas.

Continuous records of soil moisture conditions within a desert locust breeding area have not been published, although some are available within the breeding area of the Australian plague locust (Clark ibid) which breeds in conditions not too dissimilar from those pertaining to semi-arid India. These records show that it is only for short periods that the soil moisture exceeds 5% and although water-logged for short periods even after heavy rain it seldom was above 15%.
REFERENCES


Fig. 24. The Rajasthan Desert, showing regional sub-divisions, selected rainfall stations and the frequency of monsoon breeding (July-Dec.) by the desert locust.
CHAPTER 2
RAINFALL AND BREEDING IN THE RAJASTHAN DESERT, INDIA

i. Geographical Description of the Area.

The area chosen for the detailed study lies entirely within India and is bounded by the Rann of Cutch in the south, the Aravalli Range in the east and the River Sutlej in the north and by the Indo-Pakistan border in the west. Pithawalla (1948,1952) divided the region into four:

i. The Thar.
ii. The Pat.
iii. The Ghaggar Plain.
iv. The Steppe Desert and the Luni River Basin.

In the south-west, bounded in the west by the Lower Nara River lies the area known as the Thar, which is a region of longitudinal sand-dunes. These lie in a SW-NE to WSW-ENE direction, i.e. parallel to the direction of the south-west monsoon winds; they are mainly between 30 and 45 metres high, reaching a maximum height of over 150 metres. The alluvium in the flat valleys between the parallel ridges of sand is readily cultivable when moistened by the showers of rain which fall during the summer months. The southern part of this region adjoins the Rann of Cutch and is frequently flooded by sea as well as fresh water during the south-west monsoon season. This results in the formation of a series of lakes. However, during the dry season the water-table recedes to some 3.5 metres or more below the surface.

Further inland, in the region known as the Pat, where
Fig. 25. Normal dates of onset and withdrawal of the southwest monsoon (after Chattergee, 1955).
the wind force is not so great, the dunes become transverse to the south-west wind. Here the landscape is more rugged but not so high as in the Thar. The loose sandy soil covers fine clays and silts which are impervious, and so there is no downward percolation of water from the streams, which tend to form pools and lakes. Those formed near the Eastern Nara are of fresh water but most of the others are saline. Embankments now protect this area from flooding by the Indus but the flood waters from the Eastern Nara are still used for cultivation.

Further north still, in the Ghagar Plain, are a large number of dry river beds and ancient channels filled with firm loamy soils and bounded by ridges of sand. These valley floors are very fertile when moistened by rain.

The north and west fringes of the Rajasthan Desert are known as the Steppe Desert. This area is about $1/3$ sand covered, by dunes of the transverse type, and $2/3$ rocky plateau. The Luni River system runs through this area and during the dry season it becomes a series of saline streams and dry channels. During this season there is a reversal in the downward flow of sub-soil water leading to the deposition of salts on the soil surface.

ii. Climate of the Rajasthan Desert. (after Pramanik (1952) and Pramanik and Hariharan 1952)

The climate of this region can be divided into four seasons:

- December to March: north-east monsoon, cold season.
- April and May: transitional period of hot weather.
Fig. 26. Average conditions of wind and humidity during July and August, 1 and 3 km above north-west India and Pakistan. (after Pramanik, 1952)
June to September: south-west monsoon, wet season.
October and November: retreat of the south-west monsoon.

During the cold season from December to March this area is under the influence of the north-east monsoon. The mean maximum temperature is 20-25°C and the mean minimum temperature 3-10°C. There are, however, cold waves associated with westerly depressions crossing the area which can bring the temperature of individual days as low as -4°C. During this season about 5% of the annual rainfall total is received and is associated with a few of the 4-5 depressions which enter the area from the west each month. The relative humidity is 50-60% in the morning falling to 25-35% during the afternoon.

During the transitional period of April and May the temperature is at its maximum; mean maximum for May 41-42°C and mean minimum 24-27°C. During heat waves the temperature frequently rises to over 49°C. Dust storms are frequent during this period and although there are a few thunderstorms, precipitation and humidity are low (R.H. 35-60% in morning and 10-30% in the afternoon).

The average dates of the arrival of the south-west monsoon in India are shown in fig. 25, and show that it usually arrives in this area in the first half of July. Diagrams of wind and humidity (fig. 26) show that the layer of the moist southwesterlies is a shallow one and is overlain by dry subsiding air. The result is that except for a shallow layer the south-west monsoon current only
Normal annual rainfall in tracts of Rajasthan and neighbouring tracts (after Ramdas 1952).

Fig. 27

Normal number of rainy days in Rajasthan and neighbouring tracts (after Ramdas 1952).

Fig. 28
Key to place names in Figs. 27 and 28.

<table>
<thead>
<tr>
<th>PAKISTAN</th>
<th>INDIA</th>
</tr>
</thead>
<tbody>
<tr>
<td>FWR Peshawar</td>
<td>AMB Ambala</td>
</tr>
<tr>
<td>FSN Fort Sandeman</td>
<td>DLH Delhi</td>
</tr>
<tr>
<td>QTA Quetta</td>
<td>AGR Agra</td>
</tr>
<tr>
<td>MLA Multan</td>
<td>GWL Gwalior</td>
</tr>
<tr>
<td>DIK Dera Ismail Khan</td>
<td>JHN Jhansi</td>
</tr>
<tr>
<td>LHR Lahore</td>
<td>NGP Nagpur</td>
</tr>
<tr>
<td>HYD Hyderabad</td>
<td>AKL Akola</td>
</tr>
<tr>
<td>KRC Karachi</td>
<td>IND Indore</td>
</tr>
<tr>
<td>JGB Jacobabad</td>
<td>RJK Rajkor</td>
</tr>
</tbody>
</table>
penetrates into the desert areas intermittently and consequently the rainfall is scanty. The semi-arid area where the mean annual rainfall is between 250 and 500 mm lies on the edge of this anticyclonic circulation of the upper air and a deeper layer of the moist air penetrates this region causing more rain to fall although it is still not heavy.

With the arrival of the rains the temperature falls, although in the north it still reaches 46°C occasionally. The humidity is 70-80% in the morning and 40-60% in the afternoon. Following the withdrawal of the south-west monsoon in September, hot dry weather sets in until October when the temperature falls, the humidity is 50-60% in the morning falling to 20-30% in the afternoon.

iii. Rainfall in the Rajasthan Desert. (after Ramdas 1952, Pramanik 1952 and Ramanathan 1952)

The mean annual rainfall of this area varies from less than 125-760 mm, and its distribution is shown in fig.27. The number of days in which more than 0.25 mm falls varies over the area from about 5 to 50 (fig.28). About 90% of the mean annual rainfall falls during the south-west monsoon season from June-September. Ramanathan (1952) gives the mean annual rainfall for West Rajasthan as 282 mm, of which 257 fall during the summer months, the corresponding values for south-west Punjab are 249 and 175 mm and for Sindh 155 and 130 mm. To demonstrate the great variability of rainfall from year to year he showed the departure of each year by a defined amount from a 50 year normal and the
Fig. 29. Number of years in which rainfall of west Rajasthan and Sind differed from the average in a total of 50 years. (after Ramanathan, 1952)
results for Sind and west Rajasthan are shown in fig. 29.

Pramanik (1952) found that the coefficient of variability for the stations in the arid regions where the mean annual rainfall is under 250 mm, varied from 50–90 and were between 40 and 60 in the semi arid areas where the mean annual rainfall is between 250 and 500 mm.

Most of the rain falling during the south-west monsoon season in this area is associated with disturbance from the Bay of Bengal. According to Pramanik (ibid):—

"When a low or depression moves north or north-westwards through east Madhya Pradesh and Vindhya Pradesh, rain generally occurs in east Rajasthan with little rain in west Rajasthan. If a disturbance moves up to west Madhya Pradesh and Madhya Bharat, and then recurves north or north-westwards, good rain occurs in east Rajasthan and some rain in west Rajasthan. When a disturbance moves over to Rajasthan, well distributed rain occurs over most of Rajasthan. In cases when a depression follows a more southerly course and moves through Gujarat, only southern portions of Rajasthan, particularly of east Rajasthan get rain.

Only about 5% of the annual rainfall occurs during the winter in Rajasthan. During the winter or early spring, if secondaries of western disturbances pass through S.W. Punjab, we get some rain in east Rajasthan, but little rain in west Rajasthan, but if any depression sticks over S.W. Punjab or passes through Rajasthan, we get some rain also over west Rajasthan. If the secondary moves towards Kathiawar we generally get a little rain in east Rajasthan but very little rain in west Rajasthan..."

iv. Season and Frequency of Infestation by the Desert Locust.

The locust infestation normally begins in this area in May, i.e. towards the end of the dry season, and breeding coincides with the wet season during which there is a good cover of vegetation both natural and from cultivations
Fig. 30. Map showing the position of the rainfall stations within the tehsils.
within the area. An examination of the frequency maps of this area show it to be one of medium and high frequency breeding. The frequency of breeding within each of the sub-divisions (see fig. 24) shows no significant regional differentiation.

The rainfall stations selected for the detailed studies were chosen to represent conditions within the natural sub-divisions and were also in typical locust habitats. Help was obtained in choosing these 20 stations from research workers familiar with this area.

v. Data Available.

Daily rainfall values for Indian meteorological and rainfall stations are available and the data for the years 1950-1954 were collected for 20 selected stations in the Rajasthan Desert area of India. The locust data available in London for that period, except for the month of July 1954 when the full report was at hand, are the fortnightly summaries produced from the data sent to the Department of Agriculture in New Delhi. These summaries list the locust infestations according to the administrative areas affected. This means that the position within the tehsil (the smallest administrative unit in this area) is not known. The area of the tehsil varies from about 5,000 sq. km. in the cultivated areas to 16,000 sq. km. in the desert areas of Rajasthan (see fig. 30).

vi. Method of Treatment of Data.

The daily rainfall values for the 20 selected stations
together with the locust data for the tehsil in which the rainfall had been recorded, were plotted in the form of a table, with a column for each of the rainfall stations. The rainfall and locust data for May to October were listed chronologically in the columns. It was then possible to read from these tables the amount of rain that had fallen on any particular date and when any reported locust activity had occurred. These rainfall and locust data were examined for evidence of an association between rainfall and breeding in the area and also for any limiting value or values of rainfall that could be found.

For the purposes of presentation within this thesis it was found necessary to convert these tables into histograms. As far as the locust data were concerned, this did not present many difficulties. It was possible to count the number of stations recording locust activity on any one day and plot this total against the appropriate date on the diagram. Initially the locust data were divided into five categories:

i immature swarms.
ii maturing swarms or those of mixed maturity.
iii mature swarms.
iv swarms of unknown maturity.
v ovipositing swarms.

Later it was found convenient to combine the first two categories and they are shown combined in the diagrams. The ovipositing swarms were plotted on a separate graph so that they stood out clearly. Where the date on which the laying occurred was in doubt, e.g. in 1953 most of the data
were known only to the nearest week or fortnight, that section of the histogram has been shaded distinctively.

The reduction of the rainfall data into the form of a histogram presented many more problems. As with the representation of the locust data there was little possibility of showing the regional pattern of the reports. Therefore it was decided to note any significant factors of this nature in the text.

There are several ways in which the rainfall data could have been plotted:

i plotting the average daily rainfall of the 20 stations.
ii plotting the actual amounts of rainfall in the form of a dispersion diagram.
iii plotting the total amount of rainfall received at the 20 stations.

The first method using the average rainfall at the stations was precluded as it was felt that the average was not a very representative figure as frequently only a small number of the stations recorded any rainfall and amongst those that did, an appreciable degree of variability was present. Of the other two methods the second is perhaps potentially the better as it would enable the exact amounts of rainfall to be seen, but however with the omission of any information on regional distribution of this rainfall and the locust data such a degree of accuracy loses much of its value. Thus the third method which was the easiest and quickest to construct was selected and although it gives
Fig. 31, 1950.
Fig. 31. The association between rainfall and swarm activity at selected stations in the Rajasthan Desert, 1950.
Fig. 52. The association between rainfall and swarm activity at selected stations in the Rajasthan Desert, 1951.
Fig. 33. The association between rainfall and swarms activity at selected stations in the Rajasthan Desert, 1952.
Fig. 34. 1953.
Fig. 34. The association between rainfall and swarm activity at selected stations in Rajasthan Desert, 1953.
Fig. 35, 1954.
1954

Fig. 35. The association between rainfall and swarm activity at selected stations in the Rajasthan Desert, 1954.
a somewhat qualitative picture of the rain falling over the area as a whole, this was felt to give an adequate representation of the facts. The final diagrams (fig. 31-35) consist of three superimposed histograms, one of rainfall and two of locust data.

vii. Sub-Division of the Locust Data.

The period from May to mid-October was chosen to include the period of influx of desert locusts into the Rajasthan Desert which usually takes place in mid-May and also the end of laying in any one season.

<table>
<thead>
<tr>
<th>Year</th>
<th>First Swarm Report</th>
<th>Last Date of Laying</th>
</tr>
</thead>
<tbody>
<tr>
<td>1950</td>
<td>17 May</td>
<td>12 Oct.</td>
</tr>
<tr>
<td>1951</td>
<td>13 May</td>
<td>7 Sept.</td>
</tr>
<tr>
<td>1952</td>
<td>15 May</td>
<td>4 Sept.</td>
</tr>
<tr>
<td>1954</td>
<td></td>
<td>26 Oct.</td>
</tr>
</tbody>
</table>

It is apparent at once from these diagrams that the locust data can be divided into three main sections. The first of these consists of the arrival of swarms of all maturities in the area and is succeeded by the second period, one of breeding, during which laying is prevalent at most of the stations and very few if any immature swarms are seen; which is followed by a time when there are very few swarm reports but hopper bands are present; finally there is the third period which in some years is characterised by reports of immature swarms and in others by a second period of laying.

viii. Association of these Sub-Divisions with the Pattern of Rainfall.

As can be seen from the diagrams these periods do not occur at exactly the same time each year and it is possible
### TABLE 9

**INDIA, RAJASTHAN DESERT. Association between rainfall and breeding**

<table>
<thead>
<tr>
<th></th>
<th>1950</th>
<th>1951</th>
<th>1952</th>
<th>1953</th>
<th>1954</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>FIRST SHOWERS</strong></td>
<td>MAY-JULY 5</td>
<td>MAY-JULY 19</td>
<td>MAY-JULY 16</td>
<td>MAY-JULY 5</td>
<td>MAY-JUNE 26</td>
</tr>
<tr>
<td>arrival of swarms I</td>
<td>May 17</td>
<td>May 13</td>
<td>May 15</td>
<td>May 15</td>
<td>May 16-31</td>
</tr>
<tr>
<td><strong>BEGINNING OF MONSOON RAINS</strong></td>
<td>JULY 6/7</td>
<td>JULY 20</td>
<td>JULY 17</td>
<td>JULY 6</td>
<td>JUNE 26</td>
</tr>
<tr>
<td>beginning of laying II</td>
<td>July 11</td>
<td>July 31</td>
<td>July 7</td>
<td>July 1-16</td>
<td>June 19-27</td>
</tr>
<tr>
<td><strong>BREAK IN RAINS</strong></td>
<td>AUG. 15-28</td>
<td>AUG. 21-31</td>
<td>AUG. 29</td>
<td>JULY 23-30</td>
<td>AUG. 13-SEPT 1</td>
</tr>
<tr>
<td>first new a) actual swarm</td>
<td>not reported</td>
<td>Aug. 16-31</td>
<td>Aug. 22</td>
<td>Aug. 21-28</td>
<td>Aug. 1?</td>
</tr>
<tr>
<td>b) calculated</td>
<td>Aug. 29</td>
<td>Sept. 18</td>
<td>Aug. 25</td>
<td>Aug. 24</td>
<td>Aug. 7</td>
</tr>
<tr>
<td><strong>FURTHER RAIN</strong></td>
<td>AUG. 29-SEPT 30</td>
<td>SEPT 1-5 at 1 station</td>
<td>NONE</td>
<td>JULY 23</td>
<td>SEPT 23-30</td>
</tr>
<tr>
<td>a) laying from New swarms III</td>
<td>Sept. 7</td>
<td>Sept. 16-31</td>
<td>Aug. 22</td>
<td>Oct. 1-15</td>
<td>Sept. 9</td>
</tr>
<tr>
<td>b) immature from</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>WITHDRAWAL OF MONSOON</strong></td>
<td>OCT. 1</td>
<td>SEPT. 6</td>
<td>AUG. 29</td>
<td>SEPT. 24</td>
<td>OCT. 1</td>
</tr>
</tbody>
</table>

- **New swarms III a)** from Sept. 7
- **New swarms III b)** from Sept. 16-31
- **New swarms III c)** from Aug. 22
that such differences may be associated with variations in
the pattern of the rainfall. The main events for these
five years are summarised in Table 9.

a) Onset of the Monsoon rains followed by Maturation and
Oviposition.

In most years it can be seen that the onset of the
monsoon rains is shortly followed by the first reports of
laying. The delay before oviposition was recorded was 4
days in 1950, 11 days in 1951 and between 11 and 26 days
in 1953. In 1952 and 1954, however, some breeding occurred
before the break of the monsoon. In 1950 there was a
report of breeding at Nagaur during the first week of July.
It is not stated whether this was a report of a laying swarm
or of hopper bands, but in any case it is probable that
this breeding was associated with the rainfall which
occurred at the beginning of June and which at Nagaur
amounted to 21 mm. within an eight day period. In 1952
breeding began on July 7 in Sardarshahr, Churu and Jodhpur
tehsils about a week after the end of widespread rain in
these areas. In 1954 the early laying was in Suratgarh tehsil
where two falls of over 25 mm. had been recorded within a
fortnight of the layings.

This suggests that amounts of rainfall of this order
produce conditions suitable for oviposition to the mature
swarms which enter the area from nearby breeding grounds
in these instances probably from Iran, Afghanistan and
Pakistan during the period of high temperatures and low
humidity which proceed the break in the monsoon. The conditions prevalent at these times, however, do not appear to be suitable for producing the maturation of the young swarms entering the area, a phenomenon which would appear to be triggered off by the onset of the monsoon rains, for it is only in 1954 that there are any appreciable number of reports of immature swarms after the onset of the monsoon. This was almost certainly caused by the continued entry of young swarms from the nearby areas of spring breeding in Pakistan and Afghanistan long after the break of the monsoon, and not by the conditions being unsuitable for maturation. It should be noted that the break in the monsoon is not only characterised by precipitation but also by a rise in humidity and fall in temperature. These climatic changes are closely followed by changes in the vegetation and thus of virtually the entire environment of the locusts.

b) Rainfall and Maturation of Fledglings 'in situ'.

Another feature to notice in these diagrams is that maturation sometimes occurs 'in situ' of the fledglings produced from the first group of egg-layings. A line has been added to the diagrams to indicate the date when fledging can be expected calculated from the knowledge of the length of incubation and hopper development in this area. Thus attention is drawn to the time when the weather conditions are likely to be of importance from this point of view. During these five years, maturation followed by laying occurred on three occasions 1950, 1953 and 1954, but
in 1951 and 1952 there was no sign of maturation of these swarms until the following spring. Turning to the weather, and in particular the rainfall at these periods, it should be noted that there was very little rain after August on the occasions when the swarms remained immature. In 1951 when the rainfall amounted to just over 25 mm. at Nagaur (the only station reporting rain) there is some indication from subsequent reports of hatching that laying continued until the end of this rainy period, but as can be seen from the diagram the newly formed swarms did not mature.

Thus it would appear that there is some association between the onset of the monsoon rains and maturation and the beginning of laying and also between the later rains and the second period of laying.

ix. Limiting Values of Rainfall associated with Oviposition: A Study of Cumulative Rainfall preceding First Recorded Oviposition.

It had been suggested that some indication of the limiting amounts of rainfall which precede breeding might be found by a study of the cumulative rainfall before the first laying. It was found most convenient to construct graphs of cumulative rainfall starting at January 1st. To these graphs was added all the recorded locust data for that area. The locust data which were plotted on these graphs relate to the tehsil in which the rainfall station is situated. From this it can be seen that the distance of the swarm from the rainfall station is not known with any great degree of accuracy.
A
Swarms recorded in Barmer tehsil

Maturity of swarms
1951   immature     unknown
      mature       egg-laying

1950

B
RAINFALL

January    February    March    April    May    June    July    August    September    October    November    December

Cumulative Rainfall

1950

1951

Rainfall in mm

275

Date?
Frequently it was found from subsequent reports of hatching that the first layings had not been reported and plotting the data in this way meant that allowance could be readily made for this factor without the rainfall data having to be replotted. This method of plotting the rainfall data also enabled comparisons between places to be made at any one date.

These graphs were plotted for the years 1950, 1951 and 1954 and fig. 36 shows atypical example of them. During these years there were 22 occasions when it was probable that the first date of laying was recorded and another 9 when the subsequent data allowed it to be calculated with some certainty. The results are summarised in Tables 10, 11 and 12.

Popov's laboratory experiments and field observations on the depth of penetration of moisture (see chapter 1) have indicated that a rainfall amount of 6 mm. moistens a depth of soil just sufficient for oviposition to occur. However, in the laboratory moisture simulating a fall of rain of 5 mm. evaporated in the subsequent 24 hours, indicating a rate of evaporation of at least 5 mm./day. In the field with rates of evaporation exceeding 5 mm./day (Rajasthan 7 mm./day) a dry layer which greatly reduces evaporation is formed after 8-10 mm. have been lost. Thus to enable oviposition to occur, certainly a fall exceeding 2 days evaporation i.e. 14 mm. would have to occur. In the laboratory oviposition did not occur until
at least 10 mm. of moisture had been added to the sand. Of this amount a loss of about 5 mm. could have been expected. Thus it might be suggested that a fall of about 19 mm. (5 mm. + 2 days loss by evaporation) would cause conditions suitable for oviposition in the field.

A single fall of rain of at least this amount or falls on consecutive days amounting to 19 mm. were received between 0 and 16 days before laying in all but 6 of the 31 examples. Of these 6 examples 19 mm. had been received in the 1st instance within the period 2-4 days before laying. 2nd instance within the period 7-9 days before laying. 3rd instance within the period 3-6 days before laying. On the other three occasions the total cumulative rainfall for the monsoon rains season prior to laying amounted to:

1) 14 mm. in 3 falls within the period 5-13 days before laying.
2) 8 mm. in 1 fall 8 days before laying.
3) no rainfall was recorded at the rainfall station.

As oviposition will only take place in water-moistened soil the laying in at least this last example must have taken place either after rainfall had been received at the egg-site but not at the rainfall station or possibly have occurred in irrigated land.

In India maturation among the invading swarms is associated with the environmental changes accompanying the onset of the south-west monsoon. Among the changing environmental factors at this time is the onset of the rains. As can be seen from the tables, most of the rain
between January 1st and the first recorded laying falls after the beginning of the monsoon rains and it is generally this rain that makes the soil suitable for oviposition. These first rains of the season which precede the mass maturation are always widespread and sufficiently heavy for many of the rainfall stations to have received well over 19 mm. of rainfall between the onset of the monsoon rains in Rajasthan and the first recorded laying dates (see Tables 10, 11 and 12). For this reason there are few instances when the cumulative rainfall before the first recorded laying date are close to the minimum amount determined experimentally in the laboratory or to that suggested as feasible under field conditions. Mature swarms of an earlier generation do, however, sometimes enter this area with the immature swarms from the spring breeding areas. In 1950 they were recorded as laying in an area which had received 21 mm, within an 8 day period when the time interval between the rainfall and the laying was uncertain. Laying amongst these mature swarms also occurred in 1954 within 2 days of a fall of 25 mm.

The other occasions when the cumulative total preceding the first recorded laying is likely to approach the minimum amount are where the newly matured swarms enter an area which had not previously received heavy rainfall. In the 31 cases studied in these three years cumulative totals following the onset on the monsoon rains of less than 20 mm. were recorded on 5 occasions when laying occurred between
12 and 40 days after the onset of the rains. Cumulative totals of between 20 and 40 mm. were recorded on a further 5 occasions between 11 and 21 days after the onset of the rains. In the remaining 21 cases cumulative rainfall totals of over 40 mm. were recorded and laying occurred between 5 and 40 days after the rains had begun.

In none of the 31 cases in these three years did the first recorded laying take place more than 6 weeks after the beginning of the monsoon rains. The cumulative rainfall totals over this period varied greatly both from place to place and from year to year (see Table 13). When such rainfall data are used to assess the probability of breeding occurring in this area, these results show that it will not become widespread until the monsoon rains have begun, but that once maturation has occurred laying may occasionally take place in the vicinity of rainfall stations which have received less than 20 mm. of rainfall but as a rule an amount greater than this will have fallen.

REFERENCES


SOURCES OF RAINFALL DATA


CHAPTER 3
THE RELATIONSHIP OF MONSOON BREEDING AND MONTHLY RAINFALL IN INDIA AND PAKISTAN, 1938-1953.

The evidence of the association between rainfall and laying as presented in the previous chapter is not in a form which can readily be used in the interpretation and forecasting of a current situation. For this, the relevant parameters must be selected from the data which become available at that time. Each month a selection of monthly rainfall totals are sent as part of the Meteorological Services' Climat Broadcast. The association of breeding with above and below average monthly rainfall totals has been attempted, using the data of the monsoon breeding seasons for the years 1938-1953. This period was selected as the frequency of infestation during these years was found to be characteristic of a much longer period (see p.29).

1. Association between Mean Monthly Rainfall and Breeding.

To see whether or not there was an association between the monthly rainfall values and breeding, three stations were selected; Bikaner and Jaisalmer in the high frequency area and Bhuj which is further south and is in the low frequency area. The nature of the data on breeding did not enable an estimate of the amount of breeding that had taken place in the neighbourhood of rainfall station to be made. What could, however, be estimated was an
Fig. 37. The association between rainfall and breeding in the surrounding area, 1938-1953.
Fig. 37. The association between rainfall and breeding in the surrounding area, 1938-1953.
Fig. 37. The association between rainfall and breeding in the surrounding area, 1938-1953.
indication of how widespread the breeding was under different rainfall conditions and thus whether or not these factors were associated. The area selected for study comprised the nine degree squares which were centred on the one containing the rainfall station. For each year the number of these squares infested in each month was noted. These amounts were then plotted as graphs on the same chart as the graphs of rainfall (fig. 37). The similarity in the shape of these graphs suggested that there is an association between rainfall and the breeding that took place in the surrounding area. As the time lag between the beginning of the rains and laying is probably not more than a fortnight (see p. 80) the time interval of one month used in these diagrams will therefore generally be too long for any displacement of the graphs from one another to be significant from this point of view.

It is usual in this area for monsoon breeding to begin in July. At this time of year fledging occurs between 6 and 8 weeks later, and it is possible for laying by this new generation to begin in September. It is most probable that the secondary peak which is apparent in the diagrams in September/October in some years is caused by the overlapping of the breeding by these two successive generations. It was for this reason, that the data of July and August only was used in the
Accumulative percentages of degree squares infested

<p>| class mid- | sum of infested sq | accumul. | accumul. |</p>
<table>
<thead>
<tr>
<th>pt. in ins</th>
<th>of rainfall</th>
<th>f</th>
<th>f %</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>4</td>
<td>4</td>
<td>1.75</td>
</tr>
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<td>40</td>
<td>19.75</td>
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<td>2.5</td>
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Fig. 38. The association between July and August rainfall totals and the distribution of breeding in the vicinity of Bikaner, Jaisalmer and Bhuj, 1938-1953.
statistical examination of the correlation between monthly rainfall totals and breeding.

The rainfall data for these two months was divided into an arbitrary series of classes ranging from 0, 0.5 inch, 1.5 inch etc. to 26.5 inch. The number of squares infested in each month was noted and was entered against the appropriate class of rainfall. The frequency curve of rainfall against breeding was found to be skew and it was found that it could be described adequately as log-normal. This provided a log mean at the peak distribution of breeding corresponding to a rainfall of 2.71 inch lying between 95% limits of 2.69 and 2.74 inch. That is, the widest distribution of breeding is associated with monthly rainfall totals of between 2 and 3 inches, (50 and 76 mm) (see fig. 38).

ii. Locust Data.

No map was available showing the distribution and frequency of monsoon breeding in India and Pakistan for the years 1938-1953. There were, however, maps showing the records of egg-laying and hopper bands for each month of this period which had been assembled by Waloff et al (unpublished).

Breeding on the rains associated with the south-west monsoon in this area does not usually begin before July, although in a few years it does start in the latter half of June. In the course of work prepared for the Operational Research Team of the United Nations Special
### Table 4: Date of the beginning of monsoon breeding 1942 - 1961 in units of $2^\circ \times 2^\circ$ listed by the co-ordinates at the S.W. corner of the square.

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Note: Months are listed in the order of Jan, Feb, Mar, Apr, May, June, July, Aug, Sep, Oct, Nov, Dec.
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**Key:**
- a: 1-15
- b: 16-31
- ?: date unspecified
- wk: week
- unc: unconfirmed
Range of oviposition dates during the monsoon breeding seasons 1942 - 1961

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- **a**: 1-15
- **b**: 16-31
- **?**: unspecified
- **wk**: week
- **unc**: unconfirmed

Statute miles at 30°

- 0
- 100
- 200

- 65° 70° 75°
- 30° 35° 40° 45°
Fund Desert Locust Project (Magor unpublished) some
information on this point was assembled. The range of
dates were noted on which laying took place in units of
2 degrees latitude by 2 degrees of longitude for the
20 year period 1942-1961. This information has been
summarised on a map (fig.39) and is given in full in
Table 14. This shows that in these 20 years laying
started in June in 4 of these years, 1944, 1945, 1954
and 1959. Of these years two are in the study period.
Between the years 1938 and 1942 breeding began in June
only in 1941. This means that in the study period
laying began in June in 3 of the 16 years. The fledglings
from these June/July layings take from 42-58 days to
appear. In certain years these fledglings which appear
in August and September mature rapidly and eggs of a
second generation are laid in September/October. In
these years hopper bands may still be present in India
and Pakistan in December. Fortescue-Foulkes (1953)
suggests the possibility of a third generation having
been produced in 1941, an opinion not shared by Pruthi
(1951). Rao (1960) also does not mention the possible
production of a third generation in any of the years
preceding 1940 so it seems unlikely that this had
occurred in 1941. Moreover, the developmental period
for layings which take place in September is 49 days,
whereas it is 70 days for eggs laid in late October.
It therefore seems probable that the eggs and hopper bands
Fig. 40. The summer breeding area of India and Pakistan, showing the number of years in which breeding occurred in the period July-December 1938-1953 and the position of the selected rainfall stations.
seen in November and December 1941, were in fact displaying this longer developmental period and were not part of a third generation.

Frequently all the stages of development of an egg-field are not recorded. Thus, if only the reports of one stage such as egg-laying are noted, the full extent of the breeding will not be shown. As in June hopper bands from the spring breeding may still be present in India and Pakistan, the June data have not been included on the maps compiled to show the distribution and frequency of monsoon breeding in this area. They have been compiled from the reports of egg-laying by swarms and of hopper bands for the months of July to December from 1938 to 1953.

iii. The Frequency and Distribution of Monsoon Breeding in India and Pakistan.

The extent of this breeding in India and Pakistan is shown in fig. 60. In individual degree squares breeding was reported in as many as 12 of the 16 years. There is a group of squares in the desert areas of Bikaner, Jodhpur and Jaisalmer districts in India, and Bahawalpur district in Pakistan, in which breeding occurred in 10 or more of these years; the frequency of breeding decreases outside this area and in general the areas of lowest frequency are the ones furthest away from this central area of high frequency.

It was obvious from the compilation of this material
The distribution of breeding within each degree square for the months July-December and the deviation from normal of the June-September rainfall at the selected stations during the years 1938-1953.

**Key.**
- *Locusta data*
  - J = July
  - A = August
  - S = September
  - O = October
  - N = November
  - D = December

- *Rainfall data*
  - + = positive deviation from normal
  - - = negative " " "
  - *no* = " " "
  - ? = rainfall not recorded

The thick line encloses the major monsoon breeding area.
Fig. 42a and b. The distribution of swarms within each degree square for the months July-December during the years 1938 - 1953.

**Key. Locust data**
- **J** - July
- **A** - August
- **S** - September
- **O** - October
- **N** - November
- **D** - December

The thick line encloses the major monsoon breeding area.
that the distribution of breeding varied greatly from year to year. For this reason maps were drawn for each of the 16 years showing the months in which breeding had been observed in each degree square (figs. 41 a & b).

During this period there were four years (1938, 1939, 1947 and 1948) when no gregarious breeding was recorded during the monsoon rains season. The area within which breeding had occurred during the remaining years varied from 4 degree squares in 1946 to 59 degree squares in 1953. The position of the infested area also varied markedly from year to year.

As the occurrence of breeding must also be affected by the presence or absence of swarms, maps of the distribution of swarms between July and December in these years were compiled in a similar manner (figs. 42 a & b).

iv. Sub-division of the Monsoon Breeding Season.

The monsoon breeding season can be divided into three phases:

I. The influx of swarms.

II. Breeding.

III. The production of new swarms, with the possible continuation of breeding and further production of swarms.

As it is possible for gregarious populations to be produced from scattered populations and vice versa in any one year the situations listed in Table 15 are possible.
TABLE 15: The types of locust population and phase changes possible among them during the monsoon breeding season and their years of occurrence from 1938 - 1953.

<table>
<thead>
<tr>
<th>I</th>
<th>Phase Change</th>
<th>II</th>
<th>Phase Change</th>
<th>III</th>
<th>Fledglings</th>
<th>Years of Occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td>swarms</td>
<td>none</td>
<td>swarms</td>
<td>gregarious</td>
<td>none</td>
<td>swarms</td>
<td>1941, 42, 43, 44, 45, 50, 51, 52, 53.</td>
</tr>
<tr>
<td>swarms</td>
<td>none</td>
<td>swarms</td>
<td>gregarious</td>
<td>dissociation</td>
<td>scattered</td>
<td>1944, 46.</td>
</tr>
<tr>
<td>swarms</td>
<td>dissociation</td>
<td>scattered</td>
<td>gregarious</td>
<td>none</td>
<td>scattered</td>
<td>not noted</td>
</tr>
<tr>
<td>swarms</td>
<td>dissociation</td>
<td>scattered</td>
<td>gregarious</td>
<td>gregarisation</td>
<td>swarms</td>
<td>not noted</td>
</tr>
<tr>
<td>few swarms</td>
<td>gregarisation</td>
<td>swarms</td>
<td>gregarious</td>
<td>none</td>
<td>swarms</td>
<td>1940, 49.</td>
</tr>
<tr>
<td>rest scattered</td>
<td>gregarisation</td>
<td>scattered</td>
<td>gregarious</td>
<td>dissociation</td>
<td>scattered</td>
<td>1948</td>
</tr>
<tr>
<td>scattered</td>
<td>none</td>
<td>scattered</td>
<td>gregarious</td>
<td>gregarisation</td>
<td>swarms</td>
<td>1947</td>
</tr>
<tr>
<td>scattered</td>
<td>none</td>
<td>scattered</td>
<td>gregarious</td>
<td>none</td>
<td>scattered</td>
<td>1938, 39.</td>
</tr>
</tbody>
</table>
It was possible to ascertain certain facts from a comparison of the two sets of locust maps. From the maps of swarm distribution and other locust data, it was possible to ascertain that during these months no swarms were in fact recorded during the year 1938 nearer than Eritrea, 1939 nearer than West Aden Protectorate and 1948 nearer than Eritrea. However, it must be remembered that a scattered population is always present in India and Pakistan, and in certain years gregarisation can take place amongst them. In 1947, for example, the only confirmed reports of swarms were in Pakistan in September and November, and it would seem probable therefore that conditions had been suitable during the summer months for the formation of swarms by this population. In 1940, 1948 and 1949 it would appear that conditions favoured gregarisation earlier in the season as hopper bands were recorded in many districts where swarms had not been seen.

The reverse process of dissociation was also noted during this 16 year period. In 1948 the few hopper bands that had formed did not appear to retain their coherence in the adult stage since no swarms were recorded in that year. In 1944 and 1946 swarms were recorded early in the season and breeding by them resulted in the formation of hopper bands but few, if any, swarms resulted from this breeding. In years such as these it seems likely that the weather conditions, particularly
Fig. 43a. Mean monthly rainfall June-September for the selected rainfall stations.
### Fig. 43b.

Positive and negative deviations from the average rainfall at the selected stations for the months June-September, 1938-1953.
the rainfall, may have played an important part in regulating the numbers of the desert locust population.

v. Collection and Treatment of Rainfall Data.

For this reason the monthly rainfall data for the years 1938-1953 were collected for rainfall stations situated throughout the area where breeding had been recorded (fig. 40). The average monthly rainfall values for this period were then calculated for each of the 57 stations. Working maps had already been prepared for each of these years showing the months between July and December in which breeding had been recorded in each degree square. To each of these maps the seven monthly rainfall totals for the 57 selected rainfall stations were added. Another map was drawn showing the seven average monthly rainfall totals at each of the rainfall stations.

The rain with which the laying is associated generally falls in the months of July, August and September, but occasionally the rain falling in June is also effective from this point of view.

In the first instance the individual monthly totals were compared with the monthly average to see whether the departure from the average was positive or negative. The results obtained for these months of June-September are shown in fig. 43 a & b. From the results a table summarising the number of rainfall stations recording positive and negative deviations from the average rainfall was drawn up (Table 16).
<table>
<thead>
<tr>
<th>Year</th>
<th>June + - ave</th>
<th>July + - ave</th>
<th>August + - ave</th>
<th>September + - ave</th>
</tr>
</thead>
<tbody>
<tr>
<td>1938</td>
<td>35 17 0</td>
<td>13 39 0</td>
<td>5 47 0</td>
<td>2 47 3</td>
</tr>
<tr>
<td>1939</td>
<td>21 31 0</td>
<td>6 45 0</td>
<td>3 48 0</td>
<td>9 38 4</td>
</tr>
<tr>
<td>1940</td>
<td>27 25 0</td>
<td>9 44 0</td>
<td>5 47 0</td>
<td>1 47 5</td>
</tr>
<tr>
<td>1941</td>
<td>24 29 0</td>
<td>10 42 0</td>
<td>22 31 0</td>
<td>15 31 7</td>
</tr>
<tr>
<td>1942</td>
<td>24 40 0</td>
<td>39 14 0</td>
<td>32 19 2</td>
<td>29 20 4</td>
</tr>
<tr>
<td>1943</td>
<td>9 44 0</td>
<td>29 24 0</td>
<td>9 44 0</td>
<td>29 20 4</td>
</tr>
<tr>
<td>1944</td>
<td>16 35 0</td>
<td>36 13 0</td>
<td>40 9 0</td>
<td>9 37 3</td>
</tr>
<tr>
<td>1945</td>
<td>18 36 0</td>
<td>38 15 0</td>
<td>19 34 0</td>
<td>27 23 3</td>
</tr>
<tr>
<td>1946</td>
<td>27 25 0</td>
<td>12 40 0</td>
<td>27 25 0</td>
<td>4 46 1</td>
</tr>
<tr>
<td>1947</td>
<td>1 54 0</td>
<td>5 37 0</td>
<td>31 20 2</td>
<td>32 15 5</td>
</tr>
<tr>
<td>1948</td>
<td>17 36 0</td>
<td>21 15 0</td>
<td>19 7 0</td>
<td>6 30 0</td>
</tr>
<tr>
<td>1949</td>
<td>8 28 0</td>
<td>25 11 0</td>
<td>10 26 0</td>
<td>20 14 2</td>
</tr>
<tr>
<td>1950</td>
<td>3 54 0</td>
<td>36 19 0</td>
<td>19 36 0</td>
<td>25 19 6</td>
</tr>
<tr>
<td>1951</td>
<td>6 44 1</td>
<td>5 51 0</td>
<td>21 33 2</td>
<td>5 39 6</td>
</tr>
<tr>
<td>1952</td>
<td>24 24 1</td>
<td>23 26 0</td>
<td>21 27 1</td>
<td>0 44 5</td>
</tr>
<tr>
<td>1953</td>
<td>14 19 0</td>
<td>13 16 0</td>
<td>17 12 0</td>
<td>8 21 0</td>
</tr>
</tbody>
</table>
From this table it can be seen that in all the months during this 16 year period it was usual for the majority of stations to have recorded less than average rainfall, i.e. the distribution of monthly rainfall shows a characteristic negative skewness. Examination of the deviations from normal show that in general the higher the rainfall the more normal is the distribution, thus July and August show a more normal distribution than June and September.

vi. Postulations on the Effect of Rainfall on Monsoon Breeding in India and Pakistan.

Earlier work by Rao etc. (see pp. 57-58) had suggested:

1) that gregarisation is associated with above average rainfall.
2) that widespread and successful breeding is associated with above average rainfall.
3) that the presence of breeding in Baluchistan and Las Bela west of the medium and high frequency breeding areas during the summer months is associated with above average rainfall in this area.
4) that conversely the presence of breeding east of the medium and high frequency area is associated with below average rainfall.
5) that a second generation is associated with above average rainfall in September or possibly in August/September.

vii. Gregarisation in 1940.

In 1940 swarms were recorded in July in only 2 degree
squares, one in Bikaner District and one in Jodhpur district. Breeding began during July in both these areas and during the summer gregarious breeding became widespread and resulted in the production of many swarms.

In the vicinity of the initial gregarious breeding the rainfall conditions were as follows. In the case of the breeding in Bikaner District there are five rainfall stations in the two degree squares where the breeding began in July. At all these stations above average rainfall was received in June. In July the deviation from the normal in the two degree squares differed. In one both stations recorded below average rainfall, whereas in the other the reverse occurred. In August all the five stations received above average rainfall, and in September the rainfall was below average.

In Jodhpur district, breeding began in only one degree square in July, where it continued until October. None of the selected rainfall stations is situated within this degree square, but in three of the neighbouring squares there are a total of 5 stations. At only one of these stations was the rainfall above average in both June and July, at the others it was above average in June but below average in July. The August and September pattern was the same as in the Bikaner case, i.e. above average in August and below average in September.

Within India and Pakistan the distribution of swarms was again very limited. They were recorded in only 3
degree squares in all of which above average rains were received. Breeding followed in two of these three squares. In September breeding became more widespread along the Indo-Pakistan border. Rainfall data are not available in all the degree squares affected by breeding, but where they are available the rainfall was above average in 12 of the 16 rainfall stations in August and was below average everywhere in September. Breeding continued until October in much of the area, and November in 2 degree squares.

The distribution of recorded swarms remained very limited, until after September; only 7 degree squares had been affected and breeding had taken place in 6 of them. Fledglings would have been forming swarms from September onwards. In October, November and December, as can be seen from fig. 42, the swarms that had formed and were forming spread outside the breeding area and passed through a large number of degree squares.

**Gregarisation in 1949.**

A year with a similar locust history is 1949 when again after several years with little or no swarm activity or gregarious breeding, there was an influx of scattered locusts with possibly some swarms, and during the summer two generations were produced on the monsoon rains. In this year as in 1940 the breeding was confined to the medium and high frequency area. In 1949 no swarms were recorded until September, although gregarious breeding
had been observed from July. In the degree squares where breeding began in July, the rainfall in June and July was above average at 4 stations and below average at 3. At only one of the stations was the rainfall below average in both months. As in 1940, there was an extension of the area where gregarious breeding was taking place in September and October. There are no available rainfall data for Pakistan during this year, but in India where the data are available in either August or September, with one exception, the stations within the breeding area recorded more than average rainfall.

Conditions in 1947 and 1948.

1947 and 1948 were years when some degree of gregarisation was noted, but in neither case was it sufficient for a large number of swarms to have been produced. If the rainfall data for 1947 are examined, it can be seen that the rainfall for June and July was below average everywhere except at Bareilly in the east of the area near where there were unconfirmed reports of swarms in August. The rains were, however, above average in August and September at many stations. It may have been breeding amongst the scattered population on these rains that was on sufficient a scale for the production of the few swarms that were observed in September and November.

Gregarisation was noted at a different stage in
hopper bands were recorded in that year during July at several points in Baluchistan and Las Bela. Unfortunately in this area only the rainfall data for June are available, but in this month it was well above average (Pasni 146 mm., average 10 mm.). Elsewhere no gregarious breeding was recorded although at many of the stations above average rainfall was recorded in July and August, though not September. No swarms were recorded in 1948.

The pattern of summer rainfall in these four years did not vary greatly, and so it is possible that the reason for the variation in the locust history in these years lies in some factor other than the rainfall, possibly the supply of locusts from outside the area, for in both 1940 and 1949 the first appearance of swarms had been recorded in the areas to the west. In 1940 swarms were produced in Iran during the spring breeding and in 1949, following the rains brought during the passage of a cyclone in October 1948, there was a build up of the locust population in south-eastern Arabia and swarms were formed in February 1949.

Thus it appears that although in 1947 and 1948 there was a movement of locusts not only within India and Pakistan but also from further west, the numbers were not high enough to produce many swarms, for it was only in 1940 and 1949, when the numbers were higher and also gregarious breeding had occurred during the spring, that
Fig. 44. Contrasting annual rainfall totals at selected rainfall stations in 1941 and 1942.

B  Bikaner  M  Montgomery
Bh  Bhuj  N  Nagaur
D  Dewa  S  Sujangarh
J  Jalor  Sh  Shergarh
K  Khaba
a large number of swarms were produced in the summer breeding area of India and Pakistan and remained coherent during their displacement to the areas of winter and spring breeding.

The most important factor which appears to be different in 1940 and 1949 from 1947 and 1948 relates not to the weather within this area but rather to the supply of locusts from outside. No definite relationship between above average rainfall and gregarisation can be discerned from this treatment. For although at many of the stations situated near the breeding sites one or more months received above average rainfall, this was not invariably so.

viii. Contrasting Rainfall Conditions during Years of Widespread and Successful Breeding.

The years of widespread and successful breeding include those such as 1941 and 1942 when the rainfall conditions were very dissimilar. In 1941 most of the rainfall stations in the vicinity of the breeding had two or more months recording less than average rainfall, whereas the reverse was true in 1942 (see fig. 44).

An examination of the rainfall totals in these two years show that they differed markedly, the 1942 total being as much as 5 times that of 1941 in the north-west and the position being reversed further south in the neighbourhood of Jalor and Shergarh. Nevertheless breeding was widespread and successful in both of these years, showing that above average rainfall is not a
necessary condition.

ix. **Rainfall Conditions during Years of Monsoon Breeding in the Low Frequency Areas of Baluchistan Province.**

A feature of the summer breeding in some years is the extension into parts of Baluchistan west of the medium and high frequency area. It has been suggested (Rao 1960) that this takes place when the south-west monsoon extends further west than usual, an event which is marked by heavier than usual falls of rain. During the 16 years under discussion, breeding was present in this low frequency area in 7 years, 1943, 1944, 1945, 1948, 1950, 1952 and 1953.

In two of these years, 1943 and 1948, the hoppers present in July were the remnants of the spring breeding that had taken place in the area, and therefore will not be further considered.

In 1952, the one report was of hatching in mid-July in an area where a mature swarm had been seen at the beginning of the month. Turbat, the nearest of the rainfall stations, had a June rainfall amount of 44 mm, greatly above the average of 4 mm, and another nearby station, Panjgur, had above average rainfall, although Pasni further south received no rainfall at all in June. In July none of these stations received any rainfall.

In the other years, 1944, 1945, 1950 and 1953, the breeding recorded was more widespread and prolonged.
In 1944 it was associated with above average rains in July and August, and at some stations in September as well.

In 1945 the breeding was restricted to the area between 27° and 28°N where above average rain was recorded in July but not August. In 1950 the breeding was probably associated with the above average rainfall which was recorded in July at the stations in its vicinity.

The rainfall data available for 1953 are more limited than in other years; only those for 5 of the stations in Pakistan are available. With the exception of Pasni, the most westerly of these stations where no rain was recorded, above average rains were recorded at the other stations in at least two of the three months June - August.

There were, however, other years during which swarms were present in India and Pakistan, when the stations west of the medium and high frequency area received above average rainfall in a month and when this event was not followed by gregarious breeding. The months involved were July 1942, and August 1946 and 1951. In 1942 swarms had been present in the same area as the rainfall but breeding took place only amongst the stragglers left behind as the swarms moved eastwards. In 1946 there were very few swarms in the area at all and this may well be the reason why breeding
did not occur. In 1951 swarms had been present in the area in July, but by August when the above average rains were recorded their position was further east and so they were unable to make use of these rains.

It would seem though, that in general breeding does take place in Baluchistan when above average rains fall during the summer months. However, this factor, when considered in isolation, is a crude indicator, for as can be seen in certain years, such as 1951, the swarms do not move into the area with the weather system which brings the rain. This is especially likely to happen when the source of swarms is in the east and when breeding is already taking place there, for then flight activity is likely to be lessened.

In yet other years only a minority of the swarms are physiologically ready to oviposit. In such cases only a small amount of scattered breeding will occur, the majority of the individuals continuing their migratory flight eastwards.

x. Rainfall Conditions during Breeding in the Eastern Low Frequency Areas.

The extension of breeding east of the medium and high frequency area is a more unusual occurrence than the westward extension. It is also more restricted in extent. It took place only once in a large way during the 16 years. This was in 1942 when above average rain was in fact recorded. In other years only
one or two degree squares adjacent to the medium and high frequency area were affected. Only in 1941 was this breeding associated with below average rainfall in the infested degree square in all four months. Breeding in this area is not, therefore, always associated with less than average rainfall.

xii. Rainfall Conditions Associated with Maturation of Fledglings 'in situ' and Oviposition by Them.

The years showing a high percentage of rainfall stations recording more than average rainfall in September are 1942, 1943, 1945, 1947, 1949 and 1950. With the exceptions of 1947 when there was no gregarious breeding at all, and 1945 when the 2nd generation was confined to a small area, these years were characterised by a second generation. This, however, was also true of the years 1940, 1941, 1944 and 1953, when the majority of the stations in the degree squares affected had less than average rainfall in September. Most of these stations, but not all, had above average rainfall in August if not in September.

In 1944, however, no swarms were recorded after September. Following two months with above average rain, the September rainfall, as mentioned above, was generally below average and the second generation breeding was very localised. Pruthi (1951) thought that the few swarms which did form were dispersed during their westward migration. It should be noted, however, that there was an influx of scattered locusts in Oman.
in November which was followed by swarm reports in December in Iran and Oman. As the only other possible source of these swarms was the Yemen they were most probably the result of this second generation breeding in India and Pakistan.

The rainfall pattern and locust history up to September in 1951 was very similar to that of 1944, 1952 also closely resembled these years, but the second generation breeding was entirely absent in 1952. However, in these two years widespread reports within Indo-Pakistan of the swarms that had been produced were recorded during the last quarter of the year. Their continued presence in these months would suggest weather conditions different from those of 1944 when the swarms were dispersed or moved westwards out of the area during September.

xii. Conclusions.

From these monthly rainfall data of the period 1938–1953, it can be seen that comparison of the actual rainfall with the mean is unlikely to yield any successful method of interpreting and forecasting breeding in this area except in a few limited areas and cases. These are the possibility of breeding within the low frequency breeding area in Baluchistan and the likelihood of a second generation being produced throughout the area.

With regard to the breeding in Baluchistan, in these
16 years, summer breeding occurred in 5 of them. In all of these years when swarms were present above average rains were received in at least either June and/or July. Of the three years when above average rainfall in a month was not followed by gregarious breeding, in one, the above average rainfall in July was followed by scattered breeding amongst the stragglers left by the swarm, and in the other years the above average rainfall was received in August when the swarms had already left the area. It may therefore be suggested that the requisite conditions for gregarious breeding to occur in this area are the presence of swarms during above average falls of rain in June and/or July.

The association between above average rainfall in August and September, and the laying of eggs of a second generation, is not so clear cut. Although from the previous chapter it can be seen that rainfall is a necessary feature in the maturation of the newly produced fledgling swarms, it has been shown above that although this second breeding usually occurs where August and/or September rainfall is above average, in some areas below average rainfall in both of these months has been sufficient for breeding to occur.

All attempts to correlate breeding with climatic parameters such as has been done here, must necessarily entail the selection and generalisation of data. The nature of the rainfall in this area is sporadic.
Examination of the diagrams show that in any one degree square the stations do not necessarily show the same deviation from the normal in a month, still less do they receive the same quantity of rainfall. Particularly as mature swarms of the desert locust are able to utilise sporadic rainfall it is quite possible that the stations selected are not reflecting the conditions affecting the swarms.

Nevertheless, it may be suggested that the monsoon rain falling in the medium and high frequency summer breeding area is almost always sufficient to enable breeding to occur successfully when there is an influx of swarms. In years when there is only a small scattered population present it seems unlikely that an increase will occur in the numbers of the population sufficiently large to result in the production of swarms. For this to happen an unusually large influx of population is required; most probably too there must be a gregarious element amongst this incoming population. These results emphasise the part that the link between the various breeding areas plays in the development and continuation of the swarm infestations in the summer breeding belt of Indo-Pakistan.

In areas such as Baluchistan or months such as September when the average rainfall is low, the position is rather different. Under these circumstances evidently the mean monthly rainfall total must be close
to the lower limiting amount. Thus, successful breeding occurs only when above average rain falls.

In the low frequency breeding areas of Baluchistan, the mean monthly rainfall never exceeds 76 mm, and is usually between 5 and 25 mm. The average values for September vary considerably, but except in the vicinity of high land again does not exceed 76 mm. It seems probable, therefore, that the soil moisture conditions created by the individual falls which make up these totals are sufficient to enable successful breeding to occur.

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SOURCES OF RAINFALL DATA


Fig. 45. Daily weather and locust activity at Agadir in 1953 - 1954.
CONCLUSIONS

The monsoon breeding in India and Pakistan can be divided into 3 stages:-

1: the influx of immature swarms together with a few mature ones (probably of an earlier generation);
2: a period of breeding;
3: the production of fledgling swarms, which in some years mature and lay eggs in the region and which in others are eventually displaced to the winter and spring breeding areas.

These stages are associated with certain weather conditions. Stage 1 with the dry weather which precedes the arrival of the south-west monsoon and which is broken by an occasional shower probably associated with late westerly depressions. Stage 2 begins within a fortnight (often sooner) of the arrival in Rajasthan of the rains associated with the south-west monsoon. If at the end of stage 3 there is widespread rain, maturation of the fledglings takes place. This accounts for the variation which can occur, for in other years the new swarms remain immature until the following spring. These results confirm the findings of Rao (1960). They also show that in this area maturation occurs in the environmental conditions associated with widespread rainfall. However diagram 45 compiled from data available for the spring breeding area of Morocco demonstrate that this is not always so. A similar situation occurs in many parts of the belt of winter and spring rainfall where maturation of the swarms does not
occur for some months after they have arrived in areas where the rains have started. Rao (ibid) states that breeding does not begin in Pakistan until the mean daily temperature rises above 20°C. This could be an effect of low temperature slowing down maturation as is shown in laboratory experiments described on pages 17 and 18, or could possibly be associated with a seasonal variation in the nutritional value of the plants, for laboratory results (see page 20) suggest that not only does the food intake by locusts affect their rate of maturation, but that spring grass may increase it. In the examples from Morocco the mean daily temperatures had seldom exceeded 20°C when laying began. Further work is required to delimit values of the various environmental factors that could be regarding maturation in these areas.

Once maturation has occurred and the eggs are fully developed laying will take place within 72 hours (Popov 1958). If no suitable egg-sites are found then the eggs may be scattered on the surface of the soil. In order to develop successfully the eggs must absorb moisture from the soil. In the laboratory locusts have laid in sand where the moisture content was as low as 2% and have successfully hatched where the range was 1.3% to 25%. The lower limit for normal laying is slightly higher than that needed for successful hatching. Eggs are usually laid in moist sand that is overlain by a layer of dry sand which greatly reduces evaporation. In the laboratory
the maximum depth of this dry layer could be 8 cm. The narrowest layer of moist soil in which eggs were deposited was about 3 cm. In this case the eggs were placed horizontally, whereas they are normally laid vertically when a minimum depth of 6 cm. of moist sand is required.

To moisten this depth of soil a fall of rain of about 6 mm. would be required. However, it is unusual for the locusts to lay until the surface layer has become dry. In Rajasthan where the daily rate of evaporation has been estimated to average 7 mm./day, the dry layer (which greatly reduces subsequent evaporation) is likely to be formed after the loss of 8-10 mm. of moisture. In the laboratory when simulating rainfall, at least 10 mm. of water were required to create conditions suitable for oviposition. The rate of evaporation there was about 5 mm./day, which means that the remaining 5 mm. of water were sufficient to provide the requisite conditions. It has therefore been suggested that in Rajasthan, conditions of moisture suitable for oviposition would be formed after a fall of rain of 19 mm., i.e. 5 mm. + 2 days loss by evaporation (14 mm.). Single falls, or occasions when this amount fell on consecutive days were recorded between 0 and 16 days before oviposition in all but 6 of the 31 examples studied. Of these 6 cases there were only 3 in which the cumulative total over a period lasting up to 4 days, within a fortnight of oviposition, did not exceed this amount. In the remaining 3 cases the cumulative rainfall total
between the onset of the rains and oviposition did not amount to 19 mm. In 2 cases 8 and 13 mm were recorded and in the 3rd case no rain had been received at the selected rainfall station. As locusts will not lay in dry soil these results indicate either that the laying occurred in sand moistened by run-off or irrigation or possibly where wind erosion had removed the layer of dry sand exposing an underlying layer of moist sand. Alternatively that rainfall had occurred at the egg-site but not at the rainfall station. This is particularly likely to have occurred in the west of Rajasthan where the average rainfall is lower and is more sporadically distributed and also where the tehsils are larger.

These results do emphasize though that when mature swarms are present in an area a lack of rainfall for periods of a month or more at the meteorological stations does not preclude laying in the surrounding areas. The results also suggest that once swarms are mature laying can take place in areas where small amounts of rain have fallen, although in this area at any rate it would appear that maturation only takes place in association with the environmental changes which accompany widespread rainfall.

The distribution of gregarious breeding during the summer in India and Pakistan varies greatly from year to year. During the study period in the years when gregarious breeding was recorded it affected as few as 4 and as many as 59 degree squares. The departure of the monthly rainfall
from average in the summer breeding area of India and Pakistan would appear to be significant in only a few instances, such as September in the areas where the average monthly total is between 0 and 50 mm; or in areas such as Baluchistan where the average rainfall from June to September seldom exceeds 50 mm. For within the high frequency breeding area where the average seasonal rainfall exceeds this amount successful breeding took place in years with both positive and negative departures from the average. However, breeding in the low frequency breeding areas of Baluchistan was associated with above average falls of rain which occur in years when the disturbances associated with the south-west monsoon extended into the area. In some years though gregarious breeding did not occur when there was above average rainfall in this area, this happened either when early in the season most of the swarms present in the area had not matured or later when the source of swarms was to the east where laying had already begun with the result that flight activity was diminished and the swarms were not displaced by the disturbances.

Breeding in the eastern low frequency breeding area, where the rainfall is considerably higher, was not found to be associated with below average rainfall.

The maturation of the fledglings produced in this area and laying by these swarms was associated with above average rain falling in late August and September.

There is no unambiguous evidence that gregarisation
i.e. the production of swarms entirely 'de novo' from a scattered population occurred in this area during the period studied. Gregarisation took place in years when there had been some gregarious breeding and swarm formation in the winter and spring breeding areas to the west. It is possible, therefore, that some swarms had entered the area in these years although they were not reported. It would appear then that gregarisation in this area was associated with the influx of a large number of locusts into the area with a previous history of gregarious breeding, but it did not appear to be associated with above average rainfall.

i. Applications of this Work.

During the course of this work it became apparent that the rainfall data included in the monthly Climat broadcasts exchanged by the meteorological services of the world might be of value in assessing the prospects of breeding in an area and also in interpreting events in these breeding areas. Accordingly in 1960 arrangements were made with the Meteorological Office to have these data from the 104 relevant stations made available each month to the Anti-Locust Research Centre.

Since that time there have been occasions, such as in Pakistan March-May 1960, when these rainfall data have been of value in forecasting events in breeding areas. As a result, a request was made to the World Meteorological Organisation by the Anti-Locust Research Centre for additional stations in potential breeding areas to be
included in the Climat broadcasts. Arrangements were then made by the World Meteorological Organisation with the countries concerned, for these additional data to be included in the Climat broadcasts. Data for an additional 22 stations are now received regularly.

From the final results of this study it can be seen that in the summer breeding area of India and Pakistan, these Climat data can be of use particularly in months and areas where the average rainfall is less than 50 mm. Above average rains in the western low frequency areas in Baluchistan are very likely to be followed by breeding. Above average rains over a wide area in June might indicate the early onset of the monsoon rains which would be followed by maturation and breeding by the swarms. More often though the above average rainfall in this month was less widespread in the study period. Under such circumstances localised breeding among the mature swarms of an earlier generation may take place. Above average rains in September are likely to precede the maturation of and oviposition by the newly formed swarms.

The onset of the monsoon rains which precede maturation amongst the swarms in Rajasthan could be recognized from daily weather data, some of which (the 1200 GMT observations) are already received at the Anti-Locust Research Centre. It is possible that the use of daily rainfall values could improve further the prediction of breeding amongst a mature population in this area. For it seems probable that
breeding seldom occurs, except where falls of the order of 20 mm. have been received within a short period.

ii. Relevance of these Results in Other Areas.

It is apparent from the data concerning Morocco that the results of this study would not be applicable to that area nor probably to the rest of the winter and spring breeding areas. It is probable though that the relationship of breeding and rainfall might be similar in other areas of summer breeding in Africa and south-western Asia (see fig.16) where breeding similarly follows closely the onset of the main rains. Similar studies in areas such as the Sudan would be needed before these results could be applied to these other areas.

REFERENCES


Conversions of units used in the text

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1 metre = 3.28 feet
1 kilometre per hour = 0.62 miles per hour
1 millimetre = 0.04 inch
25.4 millimetres = 1 inch

Indian rainfall data: these have been converted from British to metric units except in the statistical examination in chapter 3, and where diagrams have been taken from other publications.
### TABLE 10.

**1950 INDIA: Rajasthan Desert. Cumulative rainfall before 1st recorded laying in millimetres.**

| Number of days before 1st recorded laying date in tehsil | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 40 | 50 | 60 | 70 | 80 | Jan 1st to A |
| **1) lst laying date recorded**                         |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Shergarh       July 11                                  | 1 | 7 | 71* | 82 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 9 | 9 |
| Bikaner        July 14                                  | - | 2* | 41 | 71 | - | 81 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 96 | 9 |
| Jaisalmer      Aug. 1                                   | - | 31* | 43 | - | 55 | - | 61 | 73 | - | 99 | - | - | 100 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 100 | 100 |

| **2) lst laying date calculated**                       |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| From recorded hatching date                            |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Sri Ganganagar  July 25                                 | 23* | - | - | 64 | 79 | - | - | 102 | 116 | - | - | 118 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 191 | - | 206 |
| Bidawara       Aug. 2                                   | - | - | - | - | - | - | - | 26* | 118 | - | - | 152 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 168 | - |
| Jodhpur        Aug. 6                                   | 17 | - | - | 20 | 21 | - | 24 | 28 | 31 | - | 53* | 53 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 53 | 56 | 156 | 175 | 176 | 192 | 204 | - | - | 208 |
| Ramgarh        Aug. 7                                   | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 27 | 50 | - | - | - | - | 50 |

Δ laying date: no rain; * single fall exceeding 19mm
| beginning of monsoon rains in Rajasthan July 6/7. |
| lat recorded laying in Rajasthan July 11. |
### Table 1.


| Number of days before 1st recorded laying date in tehsil | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 40 | 50 | 60 | 70 | 80 |
|--------------------------------------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 1) 1st laying date recorded                            |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| Barmer        | July 9       | 3  | 6  | 9  | 13 | -  | -  | -  | -  | 23 | 40 | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  |
| Jodhpur       | July 10      | 1  | 3  | 7  | 11 | -  | -  | -  | -  | 17 | 26 | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  |
| Nagaur        | July 12      | 1  | 6  | 20 | -  | -  | -  | -  | 20 | 30 | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  |
| Jaisalmer     | July 13      | 6  | 18 | 19 | 30 | -  | -  | -  | -  | 17 | 26 | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  |
| Sriganganagar| Aug. 4       | 4  | 8  | 11 | 15 | -  | -  | -  | -  | 20 | 30 | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  |

* A laying date: no rain
* single fall exceeding 19mm
* beginning of monsoon rains in Rajasthan June 26/27.

1st recorded laying in Rajasthan June 19.
<table>
<thead>
<tr>
<th>Table 12. 1951 INDIA: Rajasthan Desert. Cumulative rainfall before 1st recorded laying in millimetres.</th>
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<tbody>
<tr>
<td><strong>Number of days before 1st recorded laying in tehsil</strong></td>
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<tr>
<td><strong>1) 1st laying date recorded</strong></td>
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<tr>
<td><strong>Note:</strong> Laying date = no rain; * single fall exceeding 29 mm.</td>
</tr>
<tr>
<td><strong>Beginning of monsoon rains in Rajasthan July 20.</strong></td>
</tr>
<tr>
<td>1st recorded laying in Rajasthan 31st July.</td>
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* Laying date = no rain; * single fall exceeding 29 mm.
### Table 13.

**INDIA: Rajasthan Desert. A comparison of the cumulative rainfall received in different years before the first recorded laying.**

| Place     | Year | Date of 1st laying (a) | Number of days before the 1st recorded laying date in the table | Jan 1 to 30 | Δ | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 |
| Sri Ganganagar | 1950 | July 25                 | 23 - - 64 79 - - 102 116 - - 186 - - 158 - - 2 3 61 63 65 - - 66 69 - - 73 - - - - - - - - - - | 391 84 206 130 |
|             | 1951 | Aug. 4                  | 1 - - - - - - - - 71 - - 81 - - 39 - - 89 106 29 - - - - - - - - - - - - - | 391 84 206 130 |
| Bikaner    | 1950 | July 24                 | 23 11 71 - - 81 - - 39 - - 89 106 29 - - - - - - - - - - - - - - - - - - - | 391 84 206 130 |
| Sardarshahr | 1951 | Aug. 10                 | 3 - - 13 - - 17 - - 21 - - - - - - - - - - - - - - - - - - - - - | 391 84 206 130 |
| Nagaur     | 1950 | Aug. 7                  | 21 - - - - - - - - 59 73 - - - - - - - - - - - - - - - - - - - | 391 84 206 130 |
| Bikaner    | 1951 | July 15                 | 1 14 - - 20 - - - - - - - - - - - - - - - - - - - - | 391 84 206 130 |
| Jaisalmer  | 1951 | Aug. 2                  | 28 117 - - 152 - - - - - - - - - - - - - - - - - - - | 391 84 206 130 |
| Didwana    | 1950 | Aug. 5                  | 7 - 12 - - 27 - - - - - - - - - - - - - - - - - - - | 391 84 206 130 |
| Jodhpur    | 1950 | July 12                 | 31 143 - - 55 61 - - 73 - - - - - - - - - - - - - | 391 84 206 130 |
| Shergarh   | 1951 | Aug. 4                  | 1 - 74 - - 82 - - 18 - - 28 - - 32 - - - - - - - | 391 84 206 130 |
| Barmer     | 1950 | July 1                  | 3 6 9 13 - - 23 - - - - - - - - - - - - - - - - - | 25 61 84 206 130 |

*Δ laying dates: no rain recorded; beginning of the monsoon rains in Rajasthan.*