

THE MIGRATION OF THE DESERT LOCUST (*SCHISTOCERCA GREGARIA* FORSK.)

I. THE BEHAVIOUR OF SWARMS

II. A THEORY OF LONG-RANGE MIGRATIONS

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PART I. THE BEHAVIOUR OF SWARMS

SUMMARY

New evidence is given on the behaviour of migrating Desert Locust swarms, based upon some sixty encounters by various observers with swarms in Iran in 1943 and in Kenya in 1944. After describing the process by which a swarm launches on migration in the morning, the observations are used to illustrate the separate influence of locust condition, wind, gregariousness, the sun and landscape on the behaviour of swarms.

Migratory activity increased gradually after the last moult, but the tendency to fly reached full development when hardening of the cuticle was still not quite complete, whereas flight vigour, as shown by the ability to resist carriage by the wind, did not reach full development till later. Migratory activity became reduced again around the time of mating and egg-laying but continued until death. Special attention was devoted to behaviour in relation to wind, with recording of wind speed and height of flight as well as wind direction and the courses and tracks of the flying locusts. Close, continuous observations of single swarms and the numerical data accumulated suggested that low fliers tend to stabilize their ground speed by varying their air speed according to the wind speed, and showed that they tend to come down and even settle when the wind is too strong for them to make headway against it, to take off and rise in the air when the wind speed is lower, to orient into the wind as long as they can make headway but to turn aside and commonly to turn right round and fly with the wind when they can no longer make headway and do not settle. Rather higher fliers behaved in a parallel manner, but were distinctly less responsive to wind changes than lower fliers. When parts of the same swarm were observed over land and over water, the latter failed to respond to wind changes when the former did so. Mutual stimulation among swarm members was observed to reinforce flight activity, to make the locusts keep together and fly in parallel, thereby stabilizing the direction of the swarm as a whole (*gregarious inertia*), and to accelerate mass changes of direction initiated by external agencies such as wind. There was no consistent relation between the direction of the sun's rays and the locusts' orientation, but there was evidently some direction-stabilizing agency at work other than gregarious inertia, and reasons are given for supposing this to be a light-compass-reaction to the sun. Evidence was obtained that the avoidance of upstanding obstacles is merely a special case of a general effect, a ‘compensatory’ change of direction being caused by any gross movement across the eyes. This type of optomotor reaction is regarded as contributing to the observed tendency to fly along lanes, through trees, along shore-lines and valleys.

There follows a critical review and further analysis of the foregoing and previously published observations, temperature and moisture being considered as well as the influences already mentioned. The extremely confused picture presented by the data accumulated hitherto on flight direction in relation to wind direction, is attributed to a tendency to seek some universal relationship, without sufficient regard to the varying circumstances at the time of observation, especially the wind speed and the height of flight. When these are taken into account, there are indications of a regular system of relations between flight direction and wind direction. The wind appears to be a most important direction-determining agency which acts, not only by carrying the insects, but through the optomotor reactions of the insects to the apparent movement of the visible substrate. Migratory flight occurs as the normal, ‘spontaneous’ activity of gregarious locusts when at or near their preferred temperature. The suddenness of the *mass departure* of a swarm in the morning is attributed primarily to gregariousness. As flight activity increases with rising temperature, mutual stimulation among the locusts also

increases and finally transforms the disorderly mob of insects into a coherent swarm, for the first time able, and now obliged to move off *en bloc*.

Finally, all the available information is used in an attempt to distinguish what aspects of its behaviour are peculiar to the migrant locust, hopper or adult, and to find their underlying cause. The primary characteristic of the migrant is its locomotion, which is carried on with extraordinary persistency through each day and day after day, while other forms of activity are relegated for the time being to a quite subsidiary role. The tendency to go straight has often been regarded as an equally fundamental characteristic of large insect migrants, but it appears rather to be secondary, an outcome of the locomotory 'drive'. Locust migrants have no 'goal' and no special 'directional sense'. Their orientations are governed not by any single one but by a number of reactions, mainly of the optomotor type, to fellow-individuals, the sun, the wind and to other gross features of their ever-changing environment. What is peculiar about the migrant in this connexion is the unfamiliar *pattern* in which familiar reactions are arranged, resulting in some changes of direction, but also in an unusual amount of moving steadily in one direction. This peculiar pattern seems to be due to the combination of the migrant's peculiar neuro-physiological state in which reactions to stimuli which would arrest it are suppressed, with the peculiar pattern of its sensory experience during continuous locomotion. Thus external features which are the most constant concomitants of the moving insect, such as wind and sun and fellow-locusts, become especially effective as sources of stimulation when their relation to the insect is changed by them or by it, its reactions to them having thus a certain stabilizing influence on its direction. The migrant's tendency to stabilize its sensory relations with the environment is shared by non-migrating insects, and is no more peculiar to the migrant than are the types of regulatory reaction employed. It is concluded that the key to locust migratory behaviour, in all its aspects, is the opposition between two powerful tendencies of the insect: the tendency to locomotion and the tendency to sensory regulation. Keeping on a straight course is merely one of the ways in which this conflict is resolved.

(See p. 261 for summary of Part II.)

INTRODUCTION

The Middle East Anti-Locust Unit was formed by the Colonial Office in 1942 to organize, under the technical supervision of the Anti-Locust Research Centre directed by Dr B. P. Uvarov, control measures against the Desert Locust plague that had started in 1939-40 (see Uvarov 1943). As a member of this Unit during 1942-44 my particular task was to develop the use of aircraft for dusting adult locusts with contact poisons (see Gunn 1948*a*). The study of behaviour was envisaged as a central part of the work, since the mobility of swarms is a principal obstacle to successful attacks upon them. The observations were inadequate to solve the behaviour problem then thought to be of most immediate importance for successful attack from the air, namely, what determines the time a swarm remains at its night roosting site before flying away in the morning. This problem was taken up by a subsequent expedition (Gunn, Perry, Seymour, Telford, Wright & Yeo 1948). But the observations threw some light on other aspects of Desert Locust migration, particularly the effects of wind and of the phase of the insects.

The material on hopper migration obtained during the same period was put together soon afterwards (Kennedy 1945), mainly as a starting point for consideration of the material on adults now presented here. There was more material on adults and it was more difficult to analyze; especially so since the literature on the subject is very extensive and general principles are only beginning to take shape. However, the painstaking collation and analysis of innumerable locust reports by the Anti-Locust Research Centre in London (notably Waloff 1946*a*), the work of Rao (1942) and his staff in India, of Predtechensky

(1935*a*, 1935*b*) in the Middle East and Central Asia and of Zolotarevsky and his staff, and of Volkonsky (1942) in north-west Africa, have recently added so much to our knowledge of Desert Locust migrations that a new phase in its development can be said to have opened. Although much remains to be clarified concerning locust migration, it is already better understood than the familiar examples of migration in other insects, excepting only the army ants (*Eciton* spp.) (Schneirla 1940, 1945, 1949 and other papers cited therein).

The present work is not an attempt to review the whole subject. Its object is rather to contribute to the framework of general ideas which must be constructed before a final synthesis will be possible. The work is divided into three parts. This part, part I, is an analysis of the migratory behaviour of fully swarming locusts based on direct observations of them. New observations are quoted separately first, followed by a discussion of certain influences affecting migratory behaviour in the light of both the field observations and the relevant literature. In conclusion, the behaviour of gregarious locust migrants, both adults and hoppers, is considered as a whole in an attempt to identify what is distinctive about it. Part II utilizes the observations and deductions of part I for the elaboration of a theory of long-range migrations, which are considered to be a problem in themselves. Part III (Kennedy, in preparation) quotes some original observations on migration among non-swarming locusts and then discusses them, together with other evidence from the literature, in an appraisal of the relation between the phase of the locusts and the manner and results of their migration.

The field assistance of the following workers is most gratefully acknowledged: Messrs H. S. Darling, A. G. Hussain, Taqi Ahsan, O. B. Lean and Professor A. N. Scherbinovsky (in Iran), and Leading Aircraftman Hill and other members of the Anti-Locust Flight, Middle East, R.A.F. (in Kenya). If those in the Middle East Supply Centre and elsewhere whose administrative assistance, given in distracting war circumstances, made the work possible, are not mentioned by name, it is only because the list would be so long. Needless to say it is to Dr B. P. Uvarov that the principal acknowledgement is due, not only for originating the expeditions during which the field work was done and for supplying additional data, abstracts and translations from the files of the Anti-Locust Research Centre, considerable clerical assistance, etc., but most of all for stimulating discussions. During the years since 1944 in which this work has been in preparation I have had the benefit of much discussion with him, with my friend Dr D. L. Gunn and with Miss Z. Waloff of that Centre. Where any credit is due, they must share it. It should be understood, however, that the theories and conclusions put forward are not agreed upon and I alone take responsibility for them.

OBSERVATIONS

Locusts observed

Table 1 sets out the dates, places and types of the swarm observations to be described. A more particularized list, excluding observations on 'fledgling' and mating swarms and on swarms seen over Lake Naivasha on 23 to 24 May 1944, is given in Table 2, where the observers are also indicated. Cases not observed by the writer himself have been included only when it was possible to question the observer directly, and most of these observers were themselves locust specialists.

The observations fall into two main groups: (i) on swarms of two successive generations in the course of the spring-summer, 1943, generally northward migration through Iran (refs. 5 to 38); and (ii) on swarms of two successive generations in the course of the spring, 1944, generally northward migration through the Rift Valley Province of Kenya (refs. 39 to 53).

Small samples of the locusts observed in south Iran were collected and their elytra and femora measured on the spot. Their E/F ratios are tabulated as frequency distributions in table 3.

TABLE 1. PLACES AND DATES OF OBSERVATIONS ON SWARMS OF DIFFERENT TYPES

country	district	month and year	generation	swarms observed					
				semi-migrants		full migrants			
				fledglings	mating and ovi- positing	pink		yellow	
						no.	ref.	no.	ref.
Arabia	Oman and Dhufar	xii./42	monsoon and winter	—	—	4	1-4	—	—
Arabia	Oman and Dhufar	iv./43	first spring	—	—	1	5	—	—
Iran	Jask	iv./43	first spring	—	—	5	6-10	—	—
Iran	Bandar Abbas- Hajiabad	iv./43	first spring	—	—	5	11-15	3	16-18
Iran	Kerman-Anar- Rayin	v.-vi./43	first spring	—	4	1	19	10	20-28, 30
Arabia	Riyadh	v./43	second spring	—	—	1	29	—	—
Iran	Bam	vi./43	second spring	4	—	6	31-36	—	—
Iran	Birjand	vii./43	second spring	1	—	2	37-38	—	—
Kenya	Naivasha-Nakuru	iii.-iv./44	short rains	—	1	6	39-44	7	45-51
Kenya	Naivasha-Nakuru	v./44	long rains	—	—	2	52-53	—	—
totals				5	5	33	—	20	—
				10		53			

Locusts, apparently belonging to two successive generations, had been observed moving effectively northwards through Oman (east Arabia) at the end of 1942. Refs. 1 to 4 in table 2 cover the only dense, fully migrant swarms observed at this time. The loose formation and non-persistent manner in which most of them flew led to the conclusion that these locusts were not fully *gregaria* even in behaviour. An account of the observations made on them is therefore left for part III. However, the younger Oman locusts belonged to the generation which was held partly responsible for the winter, 1942-3, invasion of south Iran. Breeding occurred in Oman and south Iran on the winter rains, and the Bandar Abbas (south Iran coast), April 1943, sample (table 3) was taken from the new, first spring generation, at a time when these locusts had become sexually mature in their turn. They behaved like fully *gregaria* swarms, although some of them had E/F ratios that Rao (1942) would class as *congregans* or even *solitaria*.

The sample of yellow, mating locusts taken in late May 1943, from a swarm at Anar, 450 km. inland from Bandar Abbas, were more nearly *gregaria* biometrically and in appearance, although probably belonging to the same generation as the young Oman and Bandar Abbas samples. All the other locusts observed—that is, in swarms of the first spring generation in the Kerman-Anar-Rayin district (central south Iran) in May-June 1943, of the second spring generation in east Iran in June-July 1943, and of the short-rains and long-

TABLE 2. PARTICULARIZED LIST OF OBSERVATIONS ON MIGRANT SWARMS

ref. no.	date	time (local)	place	obs.	wind		locusts				remarks	
					direction	speed to (m./sec.)	colour	height (m.)	track	swarm size		density
1	19. xi. 42	1300	Muscat	LI	NW	1	grey and pink	10-200	C	medium	loose	—
2	21. xi. 42	1800	Masirah I	LI	S	1	grey and pink	0-30	N	medium	loose	many settled
3	25. xi. 42	1300	Salala	LI	?	1	grey and pink	0-100	C	medium	dense	many settled
4	21. xii. 42	1200	Dibai	JSK	SW	3	grey and pink	0-10	NE	very small	loose	many settled
5	8. iv. 43	1500	Ras al Khaima	DVF	E	17	pink	0-10	W	small	loose	part settling
6-10	13-17. iv. 43	all day	Jask	AGH	E	17	pink	0-100	E	large	loose	succession of flights
11	25. iv. 43	1800	Guhra	OBL	—	nil	pink	0-10	NW	large	loose	part settling
12	26. iv. 43	0900	Kutawad	OBL	—	nil	pink	0-100	NW	large	loose	part settling
13	26. iv. 43	1200	Gakum	OBL	—	nil	pink	30-300	W	large	loose	part settling
14	27. iv. 43	0800	Ab-i-Din	ANS	SW	1	pink-yellow	10-100	NE	large	loose	part settling
15	27. iv. 43	1400	Hajtabad	TA	—	nil	pink-yellow	50-200	C	small	scattered	—
16	30. iv. 43	1400	Sirjan	OBL	E	1	yellow	0-10	N	medium	loose	part settling
17	30. iv. 43	1500	Chashmeh Sefid	OBL	SE	1	yellow	5-15	SE	small	loose	—
18	30. iv. 43	1600	Alabad	OBL	SE	2	yellow	5-20	NW	very small	scattered	—
19	1. v. 43	1100	Guhra	OBL	SE	1	pink	0-10	W	small	loose	part settled
20	20. v. 43	10-1100	Kerman	JSK	SE	1-3	yellow	0-200	NW	medium	loose	succession of flights
21	20. v. 43	1200	Baghin	JSK	SE	1-3	yellow	0-200	NW	small	loose	succession of flights
22	20. v. 43	1500	Kabutar Khan	JSK	S	2-5	yellow	0-10	NW	medium	loose	succession of flights
23	21. v. 43	1000	Bayaz	JSK	SE	3	yellow	0-10	NW	medium	loose	succession of flights
24	21. v. 43	1100	Sherifabad	LI	S	7	yellow	10-100	S	medium	loose	down-wind short period only
25	21. v. 43	1500	Kabutar Khan	LI	SE	7	yellow	0-10	SE	medium	loose	down-wind short period only
26	21. v. 43	1600	Bayaz	JSK	SE	4	yellow	0-5	NW	small	scattered	—
27	21. v. 43	1800	Anar	JSK	SE	4	yellow	0-5	NW	medium	loose	succession of flights
28	22. v. 43	09-1300	Anar-Bayaz	JSK	SE	1-2	yellow	10-100	NW	large	loose	long succession of flights
29	24. v. 43	1400	Riyadh	DVF	SE	1	pink	0-200	SW	medium	loose	long succession of flights
30	3. vi. 43	1500	Anaristan	JSK	W	1	yellow	100-?	C	small	scattered	—
31	13. vi. 43	09-1300	Yusefabad	JSK	S	2-8	pink	0-10	N	medium	dense	—
32	13. vi. 43	1600	Yusefabad	JSK	S	3	pink	0-10	N	small	scattered	—
33	14. vi. 43	09-1500	Yusefabad	JSK	S	2	pink	0-10	NW	large	dense	—
34	15. vi. 43	1600	Burj-i-Maas	JSK	S	3	pink	0-10	N	small	loose	—
35	16. vi. 43	09-1100	Burj-i-Akram	JSK	SE	3	pink	0-5	NW	medium	dense	—
36	17. vi. 43	1400	Bidaran	JSK	S	3	pink	0-10	N	small	scattered	—
37	9. vii. 43	1500	Shusp	JSK	SW	2	pink	0-10	NE	medium	scattered	—
38	13. vii. 43	1100	Birjand	JSK	SW	3	pink	0-10	NE	small	loose	—
39	31. iii. 43	1100	Nakuru	JSK	W	2	pink-yellow	5-30	E	medium	dense	several columns
40	31. iii. 43	1200	Nakuru	JSK	W	1	pink-yellow	0-60	E	medium	dense	several columns
41	31. iii. 43	1500	Nakuru	JSK	W	5	pink-yellow	0-3	E	small	dense	—
42	11. iv. 44	1600	Nakuru	JSK	NW	3	pink-yellow	0-15	SE	medium	dense	—
43	11. iv. 44	1700	Nakuru	JSK	NW	6	pink-yellow	5-15	NW	medium	dense	—
44	13. iv. 44	1100	Njoro	JSK	S	1	pink-yellow	0-30	N	medium	dense	same as 42
45	21. iv. 44	1600	Naivasha	JSK	NW	3	yellow	5-15	SE	small	loose	—
46	21. iv. 44	1700	Naivasha	JSK	N	2	yellow	0-10	S	medium	loose	—
47	23. iv. 44	1000	Morendat	JSK	NW	1	yellow	0-30	SE	medium	dense	—
48	23. iv. 44	1600	Elmenteita	JSK	SE	3	yellow	0-15	NW	medium	dense	—
49	27. iv. 44	0900	Elmenteita	JSK	S	1	yellow	30-200	SW	medium	dense	—
50	30. iv. 44	1000	Eldalat	JSK	W	1	yellow	0-50	E	large	dense	—
51	3. v. 44	0900	Eldalat	JSK	NE	1	yellow	0-200	N	large	dense	—
52	23. v. 44	1400	Naivasha	JSK	N	4	pink	0-7	S	large	dense	—
53	24. v. 44	1400	Naivasha	JSK	N	3	pink	0-20	S	large	dense	several swarms

Key to observers' initials: LI, local informants; DVF, D. Vesey-Fitzgerald; AGH, A. G. Hussain; OBL, O. B. Lean; ANS, A. N. Scherbinovsky; TA, Taqi Ahsan.

rains generations in the Kenya highlands in March–May 1944—were fully *gregaria* in phase judging by their appearance and behaviour and by the appearance and behaviour of the hoppers from which they came.

TABLE 3. FREQUENCY DISTRIBUTIONS OF E/F RATIOS OF SPECIMENS COLLECTED IN SOUTH IRAN

place	date	sex	no. of specimens with E/F ratio:												total
			1.76– 1.80	1.91– 1.95	1.96– 2.00	2.01– 2.05	2.06– 2.10	2.11– 2.15	2.16– 2.20	2.21– 2.25	2.26– 2.30	2.31– 2.35	2.41– 2.45	2.61– 2.65	
Bandar Abbas	April 1943	M.	—	—	1	1	2	4	2	—	—	—	—	—	10
		F.	—	1	—	1	1	3	3	1	—	1	—	—	11
Anar	May 1943	M.	1	—	—	—	2	9	5	6	1	2	1	—	27
		F.	—	—	—	—	1	2	3	3	3	3	—	1	16

The start of migration

As far as could be judged, the fully migrant swarms encountered in both Persia and Kenya came to rest at night and launched afresh on migration each morning. This appears to be the normal although not the invariable pattern of their behaviour, and examination of that launching process should throw a direct light on the nature and causes of migratory behaviour. Gunn *et al.* (1948), who managed to be present at the morning departure of Desert Locust swarms on seventeen occasions, have described the launching process and, for purposes of aircraft attack, divided it into the following stages: quiescence, basking in trees, basking on ground, flying about, streaming away.

The present account, having a more general purpose, expands their scheme somewhat, although based on but a few observations and supported by very scanty records of accompanying conditions. There were four morning observations on fully migrant swarms, and a general account of the launching process will be given before considering the observations individually.

The locusts spend the night roosting off the ground on trees or shrubs if there are any such perches available. If it is warm there may be some movements in the growing light before sunrise, but noticeable activity begins after sunrise when the locusts move their limbs and then crawl slowly about. If it is dull and cool, movements may continue sluggish for hours. If it is bright, the locusts soon take up positions in the sun with their bodies perpendicular to its rays (Fraenkel 1930). This *basking* behaviour continues, among locusts not for the time being flying, from then on until the departure of the swarm. Baskers are at first mainly on perches off the ground, but as the morning progresses they collect on sunny, barer patches of ground, as sheets of massed, parallel-bodied insects. When crawling and basking become general, locusts begin to drop from their perches, the earlier ones mainly gliding but later ones fluttering down in a ragged rain of insects to the ground. As wing-beating becomes more energetic (fuller in amplitude) those taking off from trees, etc., do not at once drop to the ground, but fly along horizontally a few metres, and some of the locusts on the ground rise from it in similar short flights. Although these earliest fliers are scattered thinly through the swarm and apparently independent of one another, they may show a certain uniformity of direction.

As the number of fliers and the duration of each flight increase, mutual stimulation of locust by locust becomes noticeable, and its effect, at this stage, is to make the flights more random in direction. Chaotic *milling* begins; that is, loose, non-persistent flying with no

signs of a common orientation, but involving enough locusts together to form a thin cloud, resembling butterflies over their food-plants. The flights become steadily more energetic and prolonged and embrace more locusts. They begin to take the form of *surging*, that is, temporary and local concerted flights by flocks of insects, directions differing from flock to flock, and from time to time in the same flock. With further increase in the duration and vigour of flights the flocks grow larger, absorbing individual fliers and smaller flying groups.

At this time there are still many locusts basking in trees and on the ground. Taking off by single baskers, apparently spontaneously, can still be seen, but now whole groups of baskers take off together or in rapid procession especially when flocks of other fliers pass over.

At some time during milling and surging, 'there tends to emerge a thickening uni-directional stream' (Gunn *et al.* 1948, p. 14). The stream is not a continuous column of fliers. What happens is that, amid all the confusion, a common direction becomes increasingly apparent among individuals, groups and flocks, even when they have no evident connexion with one another. The common direction may change from time to time and the locusts concerned do not fly far, but the common direction seen at this time is naturally more conspicuous than that sometimes observed before milling has become general, for the fliers are now more numerous and stay in the air for tens or even hundreds of metres.

Finally, the pattern of movement in the swarm undergoes what is usually a rather dramatic transformation. Resettling declines markedly and the basking locusts rise up in flocks to join their fellows sweeping overhead, leading to a sharp increase in the number of locusts in the air. The fliers merge into a single great flock in the air, and at the same time they all assume the same direction and keep to it with a persistency not seen until then. Gunn *et al.* (1948) describe this as 'the beginning of a mass stream-away'. They found it was striking enough to be fixed in time within a few minutes, but that the complete evacuation of the roosting site could take an hour or two. In all the four present cases evacuation was virtually complete in 15 to 20 min. Since fairly sustained, if thin, streaming can sometimes be discerned some time before the massed stream-away of the departing swarm, it is proposed to call the former *streaming* and the latter *mass stream-away* or *mass departure*.

To sum up, the process may be tabulated as follows:

- (1) Beginning of activity—crawling.
- (2) Quiescent basking in the sun, perpendicular to its rays.
- (3) Vol-planing and hopping flights—individual and very short, but often in a common direction (thin *streaming*).
- (4) *Milling* flights—short and disorderly, by many individual locusts.
- (5) *Surging* flights—longer and by whole groups together, but with directions varying.
- (6) *Streaming*—increasingly prolonged flights in one common direction.
- (7) *Mass departure*—sustained, uni-directional flight embracing the entire swarm, basking locusts rising to join it.

It is emphasized that while the stages are given in order of their appearance, there is much overlapping. Stage 2, basking, continues through stages 3, 4, 5, 6 and into 7. The only noticeable break in the whole process is when stage 6, streaming, passes into stage 7, mass departure. Then all the earlier stages, if still evident, come to a more or less speedy end.

The duration of the stages varied considerably between different days as will be seen in figure 1.

13 April was a misty morning with thin cloud over the sun and the temperature rose slowly. Milling and surging involved only a minority of the locusts, the majority passing straight from basking into streaming and mass departure.

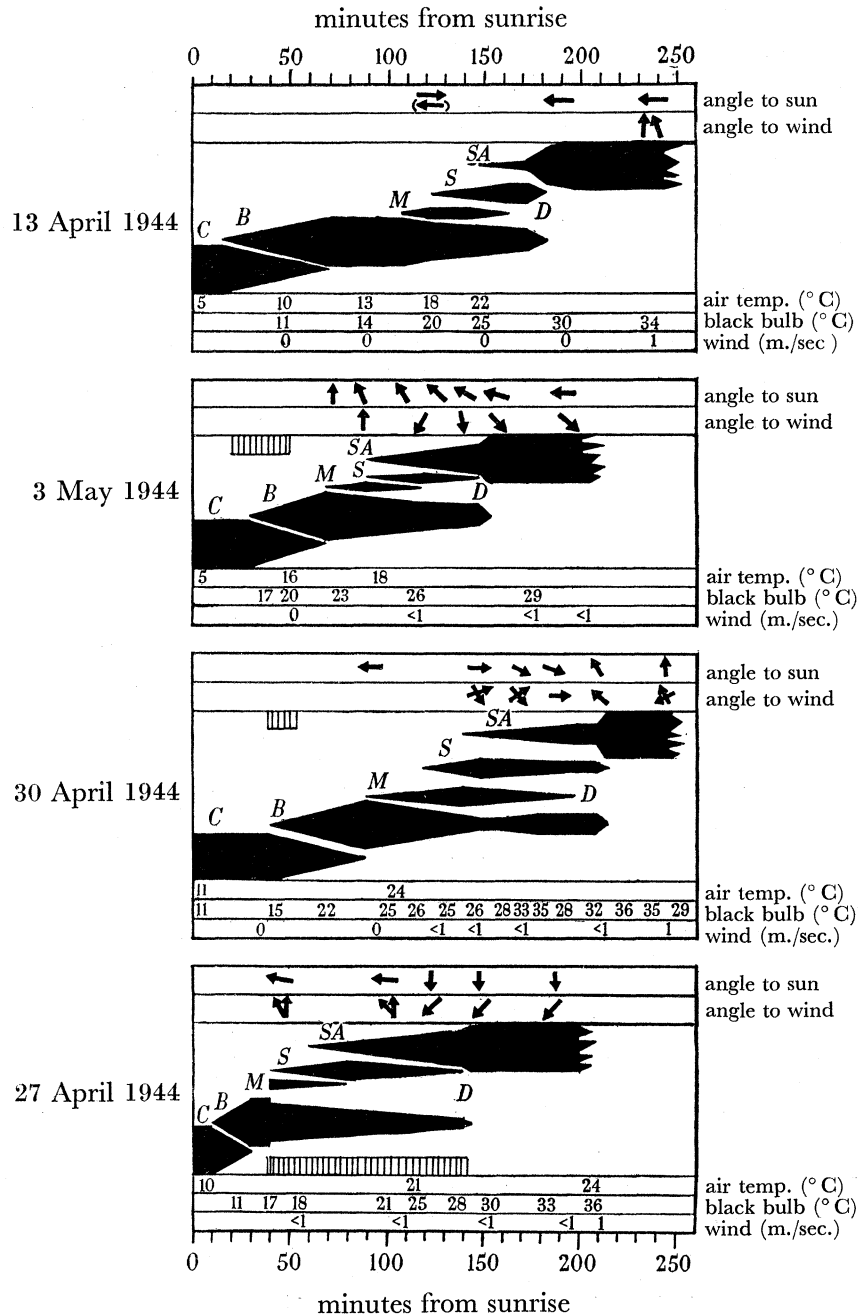


FIGURE 1. The morning behaviour of migrant swarms. The vertical width of each black strip is roughly proportional to the fraction of all the locusts visible that were engaged in the type of activity indicated. C, crawling or motionless, not basking; B, basking; M, milling; S, surging; SA, streaming-away. The time of mass departure is indicated by D. Orientations are shown along the top of each record, with the sun assumed to be at, and the wind blowing from, the top of the page. The vertically striped blocks mark the periods when aircraft were flying low over the swarm.

3 May was a clear morning and the temperature rose rapidly. Milling and surging began 40 min. earlier than on 13 April. These stages were short-lived and involved an even smaller proportion of the locusts than on 13 April, for streaming began as soon as surging, at 90 min. from sunrise. Mass departure, at 150 min., was less dramatic than on 13 April because the majority of the locusts were streaming before the final spurt of taking off and the onset of sustained flight marking the mass departure.

30 April was clear at first but the locusts were extremely wet, and basking had only just become general at 100 min. when the sun began to be obscured intermittently. Milling and surging lasted twice as long as on 13 April and 3 May with repeated mass resettling. Mass departure was delayed until over 200 min. from sunrise and after more than an hour's thin streaming.

27 April was a clear morning, but the course of events was violently altered by disturbance from low-flying aircraft. These were Avro Ansons which flew over the swarm, dusting it with dinitro-*ortho*-cresol, one after another every few minutes at heights of 3 to 10 m. Dusting aircraft had also flown over the swarms observed on 3 May and 30 April, but before basking had become general (see figure 1) and without noticeable effect on the locusts. On 27 April however, the low-flying started after basking had become general and continued for 100 min. The insecticide dosage proved to be too low to produce any appreciable kill, but each aircraft generated the most violent flight activity among the locusts, which rose in masses in *front* of the aircraft's nose, alike when the latter was delivering dust and when it was not. Milling began with the first aircraft at 40 min. from sunrise and surging immediately afterwards, followed at 60 min. by streaming. Streaming embraced more and more locusts during the next 80 min., so that the mass departure at 140 min. was not very striking, for most of the locusts were already air-borne.

On all four occasions it was observed that the common direction of streaming locusts was assumed independently by separate groups and even by isolated individuals. Sometimes individual locusts were observed to take up the stream-away direction while completely screened by vegetation from any sight of their fellows. Streaming locusts were apparently reacting in common to some external directing agency, and records were therefore kept of their orientation with reference both to the sun and the wind (figure 1), bearing in mind the conclusions drawn from observations on hoppers (Kennedy 1945) that departure directions might be connected with basking orientation.

On 13 April the departure direction was northwards, the direction in which about half the locusts were facing as they basked perpendicular to the sun's rays, but the departure direction was at the same time against the northerly wind. Locusts basking with their right sides to the morning sun took off and continued to fly with that orientation into the wind. Those basking with their left sides to the sun took off in that orientation, but once in the air and so exposed to the wind, they wheeled round into the up-wind orientation, with their right sides to the sun, as they settled down to steady flying. The wind alone might have been regarded as setting the departure direction had it not been noticed that from the very first the orientation of streaming locusts was more fixedly perpendicular to the sun than it was parallel to the wind. This swarm was kept in sight for about an hour from the time of its departure from the roosting site, for it progressed slowly owing to periods of resettling when the wind rose. During that time the wind direc-

tion was not of course rigidly fixed but frequently shifted by as much as 45° . Yet the locusts did not follow the shifts, their orientations remaining within a much narrower range of compass directions.

On 3 May, 30 April and 27 April flight directions bore no consistent relation to the wind as will be seen from figure 1. On 3 May the departure direction, like the basking orientation, was perpendicular to the sun's rays, as on 13 April, although earlier streaming locusts had not in this case been flying perpendicularly to the sun's rays. They started flying directly toward it, and the direction of streaming shifted steadily around until it was perpendicular to the rays. The up-sun direction appeared originally among the earliest vol-planing and hopping fliers before basking had become general and thus could not have arisen out of a basking orientation. On 30 April and 27 April, early, thinly streaming locusts flew in the contemporary basking orientation, perpendicular to the sun's rays, but final departure directions were parallel with the sun's rays: up-sun on 30 April after prolonged milling and surging activity, and down-sun on 27 April after equally prolonged and even more intense surging activity prematurely induced by the low-flying aircraft.

One additional point should be mentioned: individual locusts were observed to flutter their wings without taking off on 30 April and 3 May. Gunn *et al.* (1948) observed wing fluttering one morning as a mass phenomenon among densely packed Desert Locusts on one tree, among many trees similarly packed with locusts where no wing-fluttering occurred. They suggested that it was set off by jostling among the insects. The present occasions were different in that the locusts were not so densely crowded and the fluttering individuals were scattered here and there throughout the swarm, so that jostling was less likely to be what set off the fluttering. On both occasions, however, the locusts were very wet from rain (as they were also in the case described by Gunn *et al.*). On 13 April and 27 April, when there was no fluttering, the locusts were moist with dew but not encumbered by large rain drops.

Influences affecting swarm behaviour

The condition of the locusts

First among the influences affecting migratory behaviour was evidently the condition of the locusts themselves. Most of the locusts encountered during this investigation were at least several weeks old and fully hardened, but, whether pink or yellow in colour, they were not engaged in mating or egg-laying. Such swarms are listed as 'full migrants' in table 1, for whenever they were observed, during most of the hours of daylight, they were in energetic flight, implying that they flew persistently through those hours. A minority of the swarms encountered were composed either of recently moulted adults, or of sexually mature adults a proportion of which were observed mating and ovipositing. These two conditions of the locusts themselves seemed to hinder their migration. Such swarms are therefore listed as 'semi-migrants' in table 1.

Fledglings. Recently moulted adults, or *fledglings* as they have come to be called, were observed for eight successive days in June 1943 in the region south of Bam, south-east Iran. Initially, on 9 June there were still many hoppers and newly moulted adults scattered over a large area. The soft adults did not fly at all, except when disturbed, and then very briefly and feebly. There were also large concentrations of somewhat older fledglings in and around the oases. These were harder-bodied and flew readily, but were still perceptibly

softer to the fingers than yet older, fully migrant locusts. The morning behaviour of these more advanced fledglings was watched on three days: 10, 11 and 12 June 1943 (figure 2). It was very warm, as the few temperatures entered in figure 2 show. Crawling activity did not stop altogether even during the night, and basking became general almost immediately after sunrise. But there was no sustained flying, and no mass departure. A consistent direction did appear on 10 June, which is shown as streaming in figure 2, but in fact these locusts settled with every small increase of wind. Had they remained in the air they would certainly have been turned down-wind, and such alternating orientation has been described as *surging*. On 11 June, a warmer day, the locusts flew rather more uninterruptedly, rising higher in the air. On 12 June they were immobilized for most of the morning by a strong wind. They surged up-wind and down-wind during a brief lull at 130 min. after sunrise and again when the wind dropped after 320 min.

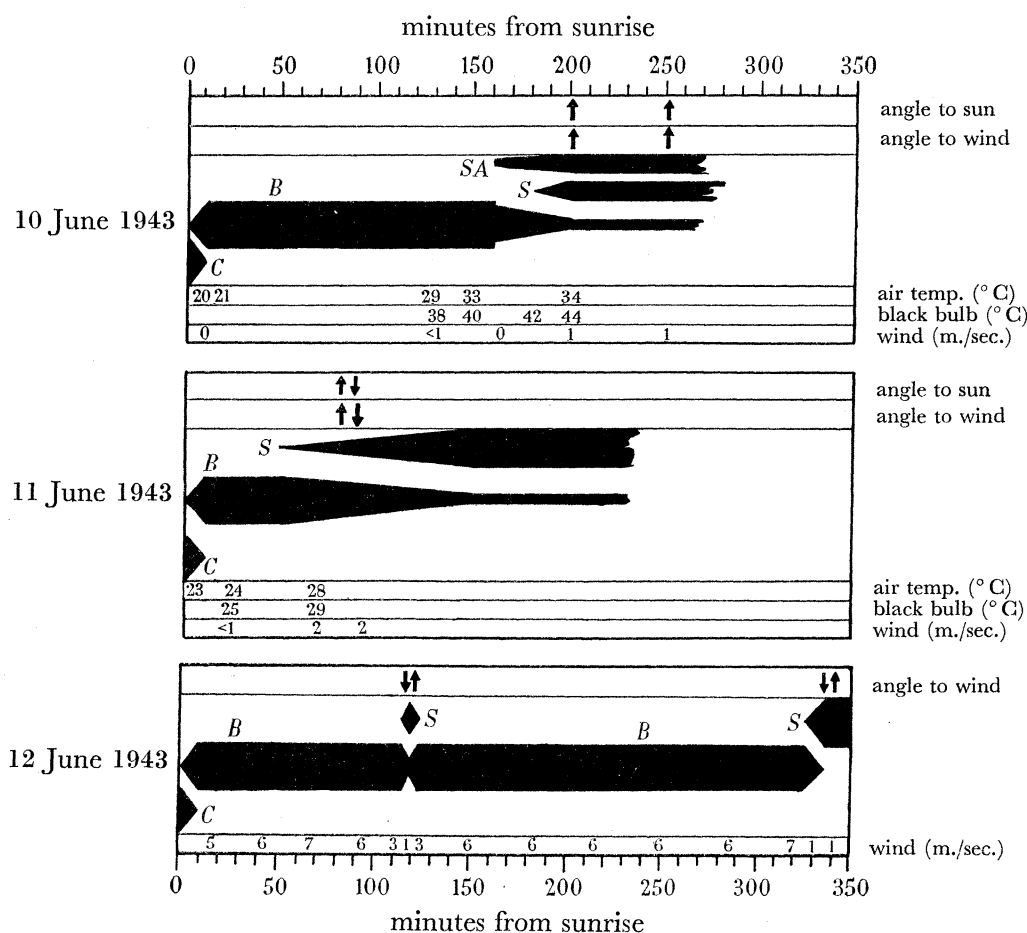


FIGURE 2. The morning behaviour of fledgling swarms. Constructed as figure 1.
Temperature on 12 June followed a similar course to that on 10 June.

The persistence and vigour of flights increased day by day. From the 9th to the 12th the locusts 'milled' and 'surged' a good deal, making little resultant progress. On the 13th they had passed into a half-surging, half-migrating stage and shifted *en bloc* to a new roosting site. By the 16th they had moved several kilometres, and it was clear that their behaviour would soon be indistinguishable from that of fully hardened, migrant swarms. It was

usually rather windy, and the fledglings flew low and against the wind. They were easily driven back, turned about and forced to settle by very moderate gusts, against which older adults could have made headway. In calm, warm periods they sometimes rose higher into the air, and then were swept back for considerable distances by opposing but quite gentle gusts.

To sum up, the fledglings were seen to develop fully migrant behaviour gradually as they hardened. Their behaviour exhibited a developmental sequence paralleling, on an extended time-scale, the morning launching process of a fully migrant swarm. Inasmuch as the wind easily carried them with it or grounded them, their tendency to fly spontaneously *en masse* seemed to develop in advance of their ability to fly strongly.

An isolated observation of fledglings taking to flight at dusk may be mentioned here. Fledglings were encountered again near Birjand, north-east Iran, on 10 July 1943. They flew very little in the daytime, many being quite soft, and flying had ceased altogether well before sunset. At dusk the sky was clear, the air temperature was 24° C, and a light wind was blowing from the north-east. A few minutes after the sun had set a large number of individuals were seen to take off one by one and fly low until out of sight. Some flew against the wind, and a few in the opposite direction with the wind. Most flew facing straight towards the bright western sky. The number of take-offs reached a maximum about 30 min. after sunset and then declined gradually until it had ceased entirely a few minutes before it would have been too dark to see the locusts against the sky. The great majority of the swarm remained where they were for the night. It was not observed whether such dusk take-offs occurred also at Bam in June.

Mating and ovipositing swarms. The behaviour of mating and ovipositing swarms was observed for several hours from sunrise on four occasions in Iran in 1943: at Anar on 22 May, at Kabutar Kahn (between Anar and Kerman) on 26 May, and near Rayin (south of Kerman) on 31 May and 1 June. Another such swarm was observed for some hours on the western shore of Lake Naivasha, Kenya, on 22 April 1944. Detailed notes were kept on the last three occasions which are illustrated in figure 3.

There was no mass departure on any of these days, but a long-drawn-out trickling away by individuals or loose groups which often flew up-wind for short distances but were repeatedly carried and thereupon turned down-wind, even by weak winds. These flights are entered as 'surging' in figure 3, but were much less dense and at first less energetic than the usual surging flights of full migrants already described. Many of the locusts were still on the ground when observation ceased, and by no means all of these were engaged either in mating or in egg-laying. Many were simply sitting quietly in the sun.

On 31 May there was little copulation and no oviposition to be seen. The swarm watched on the next morning was very possibly the same one. Numerous copulating pairs and ovipositing females with males on their backs were found in the latter swarm during the earlier part of the night 31 May–1 June. Later the cold immobilized them, and many females were found torpid with their abdomina inserted in the ground. Mating and laying became general again during the following morning while scattered fliers were leaving. This swarm, like the one observed at Anar on 22 May, contained many more males than females when inspected during the first hour or so after sunrise. Many of the females and a few of the males were found dying. Some hours later on 1 June the sexes were found to be present in

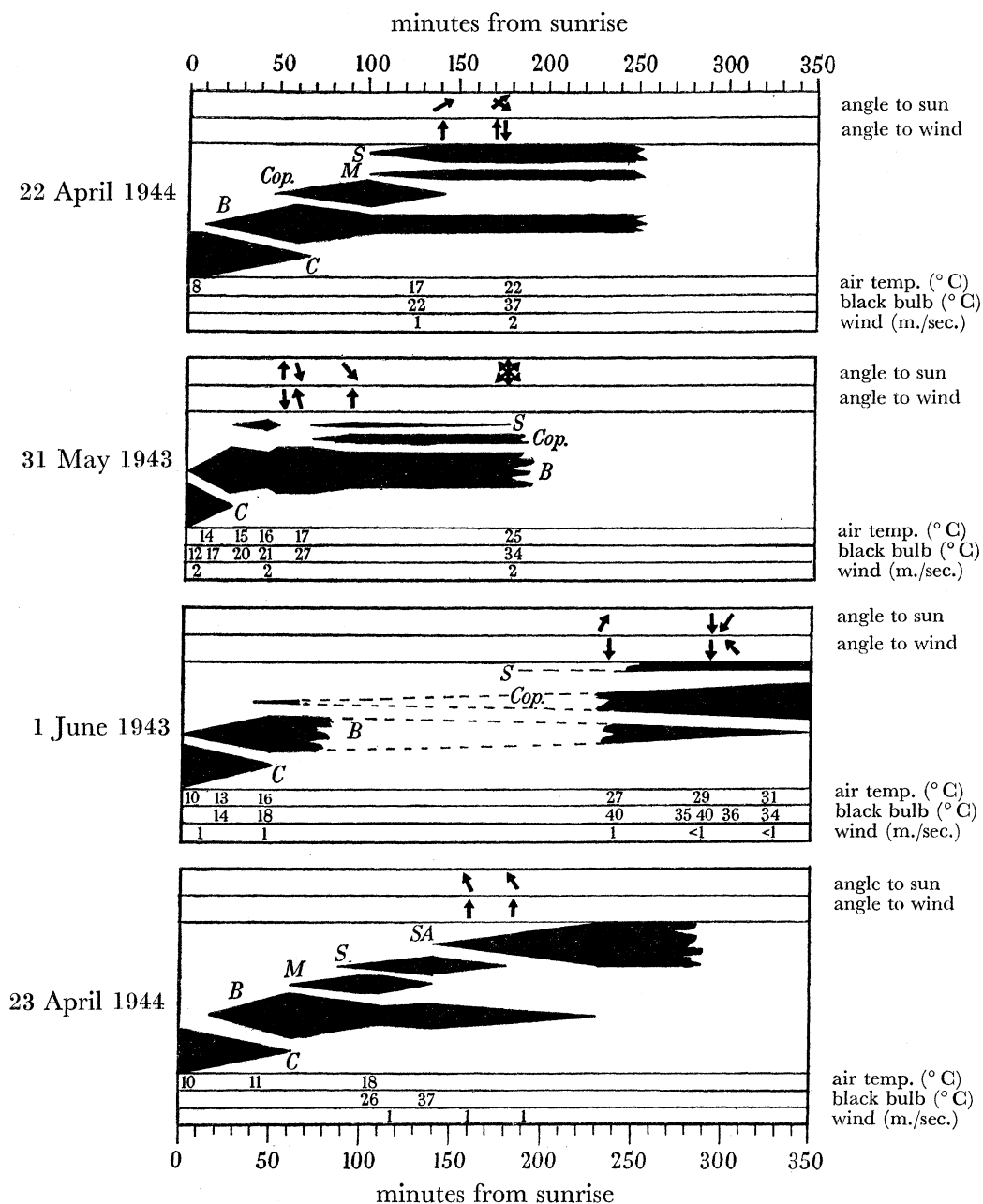


FIGURE 3. The morning behaviour of copulating and ovipositing swarms.
Constructed as figure 1. *Cop.* copulating.

nearly equal numbers among the remaining locusts, showing that it had been mainly males that had flown away. On this day the departing fliers flew sufficiently vigorously and sufficiently in a common direction, down-wind, to be described as streaming, but they did so very loosely and over a much longer time than that occupied by the mass stream-away of fully migrant swarms already described.

The swarm observed in Kenya on 22 April 1944 also streamed slowly away on the wind in this fashion. On both these days it was observed that while some fliers were streaming near the ground, others were flying to and fro higher up over the roosting site. The latter increased in number until they formed a large but very thin milling cloud of locusts. As

time went on this cloud extended higher and higher into the sky, many individuals being detectable only when the sun caught their wings as they passed between it and the observer. The high fliers eventually lost connexion with those near the ground, leaving an intermediate stratum clear of locusts and two totally different types of flying going on at the same time, uni-directional below and multi-directional above.

The swarm observed in Kenya on 23 April 1944 may have been the same one as that watched departing the previous day. Local observers believed it had been mating and laying for several days previously at various points in the vicinity, but no mating or laying was seen during the 4 hr. the swarm was watched on 23 April. This observation is included here because the locusts' behaviour was peculiar, being intermediate between that of a fully migrant swarm and that of a mating swarm. Unlike the locusts from mating swarms, these showed well-defined milling and surging behaviour and departed in a fairly thick stream against the wind without forming a high-circling detachment, and they had evacuated the roosting site altogether after 3 hr. For that reason their departure is shown as streaming in figure 3; but there was no mass departure. The departing stream was looser and more ragged than that of fully migrant swarms, basking was long-drawn-out, and the swarm took 40 min. longer to evacuate its roosting site than the slowest of the fully migrant swarms (figure 1), although the weather was warmer.

All these swarms showed a weakened tendency to take off either individually or *en masse*. Unlike fledglings, they were, however, capable of vigorous flight when pursued. The restriction of migration was associated with sexual activity, but was not simply due to the replacement of flying activity by copulation and egg-laying, for there were always many locusts not doing either of these things and still not actively migrating.

Wind

Speed of flight. When, as frequently happened, full migrants were seen flying very low into the wind, their ground speed (speed relative to the ground) seemed to show a measure of independence of variations in the wind speed. This was merely an impression, for only the wind speed and not the insects' speed was measured, but the impression was very strong. When the wind increased or decreased, low up-wind fliers did not appear to slow down or accelerate proportionately but rather to maintain a relatively unchanged ground speed in winds up to 4 m./sec. (9 m.p.h.) or more. If they did maintain roughly the same ground speed against such a range of wind speeds, the locusts must have adjusted their air speed (speed of movement relative to the air) to the wind speed. Judging by the speed of wind gusts which, suddenly meeting the locusts, carried them momentarily backwards, the cruising air speeds of locusts flying against light winds varied between 2.5 and 4 m./sec.

The impression that low fliers were regulating their ground speed by adjusting their air speed according to the wind speed, was strengthened by a further impression: that higher fliers were not so adjusting their air speed, so that their ground speed was more closely dependent on the wind speed. The fact that higher fliers appeared to be more easily slowed down and even carried backwards than low fliers in the same gust, might, of course, be attributed merely to the fact that the wind is stronger away from the frictional drag of the ground. But higher fliers appeared also to surge forward more freely when the wind dropped, which could not be explained in the same way, and suggested that they were actually

exercising less control over their ground speed, that is, maintaining a more unchanging air speed.

Amount of flying and height of flight. Low-flying migrants showed a clear tendency to regulate the amount of flying they did and the height at which they flew, according to the wind speed. Increase of wind speed to the point where down-wind orientation supervened (p. 184) did not noticeably affect the locusts if the increase was only momentary, and there was a quick return to up-wind orientation. More prolonged exposure to a wind of this or greater strength, however, led to a decrease in the height of flight or even to complete settling. If the locusts made headway against the wind at the lower flight level, owing, presumably, to the wind being slower near the ground, they flew on, keeping low. If not, they settled. Some particular incidents may be quoted to illustrate these effects.

On 20, 21 and 22 May 1943, a succession of scattered individuals and swarmlets of mature locusts (table 2, nos. 20–28) were observed moving in a north-west direction up the Kerman-Anar road against a wind of 1 to 3 m./sec. At about 1300 hr. on 22 May the wind increased to 3 to 6 m./sec. and remained at that level without any other changes in the weather, whereupon flying ceased and only settled locusts were seen for the rest of the day's journey.

On the afternoon of 24 May 1944 a large, rather loose, immature swarm was watched on the shores of Lake Naivasha. It had crossed the lake in intermittent sun, flying at 5 to 30 m. above the water and against a wind of 2 to 3 m./sec. Part of the swarm had already reached the shore and passed on over the land, when the wind increased to 4 to 5 m./sec. Thereupon most of the locusts that were over the land, especially the lower fliers, flew on against the wind and dropped lower still. For many minutes afterwards the numbers in the air over the land, and the level at which they flew, rose and fell repeatedly in inverse relation with the rise and fall of the wind speed. Then, heavy rain began to fall on them, with a drop in temperature, and some further increase in wind. The locusts dropped even lower, disappearing among the trees, and did not rise into view again. Two hours later they were found about 1 km. up-wind of where they had disappeared, showing that they had not been entirely settled during the rain, but had continued low, up-wind flight whenever the wind permitted. A similar series of descents and ascents associated with alternate periods of stronger and weaker wind, respectively, was observed over the land on the opposite (northern) shore of Lake Naivasha on the previous day.

On the morning of 31 March 1944 several small, maturing swarms (table 2, nos. 39–40) were seen near Nakuru, Kenya, flying in intermittently sunny conditions. The level of flight ranged from near the ground up to 60 m. A few hours later it began to rain rather heavily, the temperature dropped and the wind increased to a stiff breeze. Two swarms (table 2, no. 41) were seen in the rain, very probably the same as had been seen earlier. In both cases the majority of locusts were settled at any one moment, but there was constant taking off by a minority who flew strongly against the wind, mostly keeping less than 1 m. above the ground and settling again when they could not make headway. Now and then individuals rose higher in the air, but came down again as soon as the wind began to sweep them back.

The start of flying by massed fledglings on the morning of 12 June 1943 (figure 2) was delayed for a long time in comparison with what happened on 10 and 11 June 1943, solely,

it seemed, because of an unusually strong wind, for otherwise the weather was similar on the three days. As soon as the wind dropped, 'volleys' of locusts took off simultaneously at different points in the settled swarm, and the whole swarm rose quickly.

There were many observations of migrating swarms during which only one or two pronounced changes of wind speed occurred, and no quantitative records were kept. It was seldom possible to keep a migrating swarm in sight for long enough to observe the effects of repeated, large wind-speed changes on flight activity, as was done on 13 April 1944 (p. 172) and 24 May 1944 (p. 178). But it can be stated with some assurance that whenever a low-flying swarm was observed in windy weather, its flight activity (the proportion of insects flying) and its height of flight decreased when the wind rose and increased when it fell. Settling due to an increase of wind speed was evidently merely the extreme case of flying lower from the same cause.

The immediate reduction in the height of flight when the wind increased was seen only among locusts already flying within a few metres of the ground. Members of the same swarms that were flying rather higher than that also responded, but more slowly and irregularly. The effect of wind changes on swarms flying yet higher, and completely out of touch with the ground, was not observed, but it is noteworthy that there was usually little wind at ground level when fliers were seen so high.

Attempts were made to obtain more quantitative data from fledglings, whose persistent but weak flight activity meant that opportunities often arose of observing them in winds against which they could not make headway. Unlike full migrants, which were usually able to make some headway against the moderate winds prevailing during most of the observations, low-flying semi-migrants were often completely immobilized by such winds. The absence (see table 8, p. 191) of any cases of flight by semi-migrants in winds of 4 or more m./sec. illustrates the immobilizing effect of even moderate wind on these fliers.

Records were made of the flight activity of advanced fledglings on 13–14 June 1943, at Yusefabad, south of Bam, south-east Iran. They were migrating actively, but kept low and were very sensitive to wind-strength changes. Six series of minute-to-minute readings were taken of wind strength and flight activity. Two of the series are shown in figures 4 and 5. A regular relation between wind speed and flight activity could hardly be expected in these records, because the wind-speed variations were irregular and too rapid to be recorded in full. The unfaithful recording of short, high-wind-speed periods was especially misleading, for these had a noticeable effect upon the locusts. Also, the responsiveness of the locusts varied with their height, which could not be recorded conveniently at the same time.

However, the main blocks of activity (*AA*) are fairly clearly associated with weaker wind periods: 2 to 4 m./sec. in figure 4 and 0 to 1.5 m./sec. in figure 5; while the main blocks of lesser activity (*BB*) are associated with stronger periods: 4 m./sec. in figure 4 and 1.5 m./sec. in figure 5. And on a shorter time-scale, there are many cases where a decrease of wind speed is followed by an increase of locusts flying (corresponding *odd* numbers on the figures); and where an increase in wind speed is followed by a decrease of locusts flying (corresponding *even* numbers). Thus the changes in activity level seemed to depend not so much on the absolute wind speed as on changes in the wind speed, which often took effect in less than a minute. The apparent failure, according to the records, of gusts always to reduce activity instantly was partly due to the fact that although all the locusts responded to a gust, not all

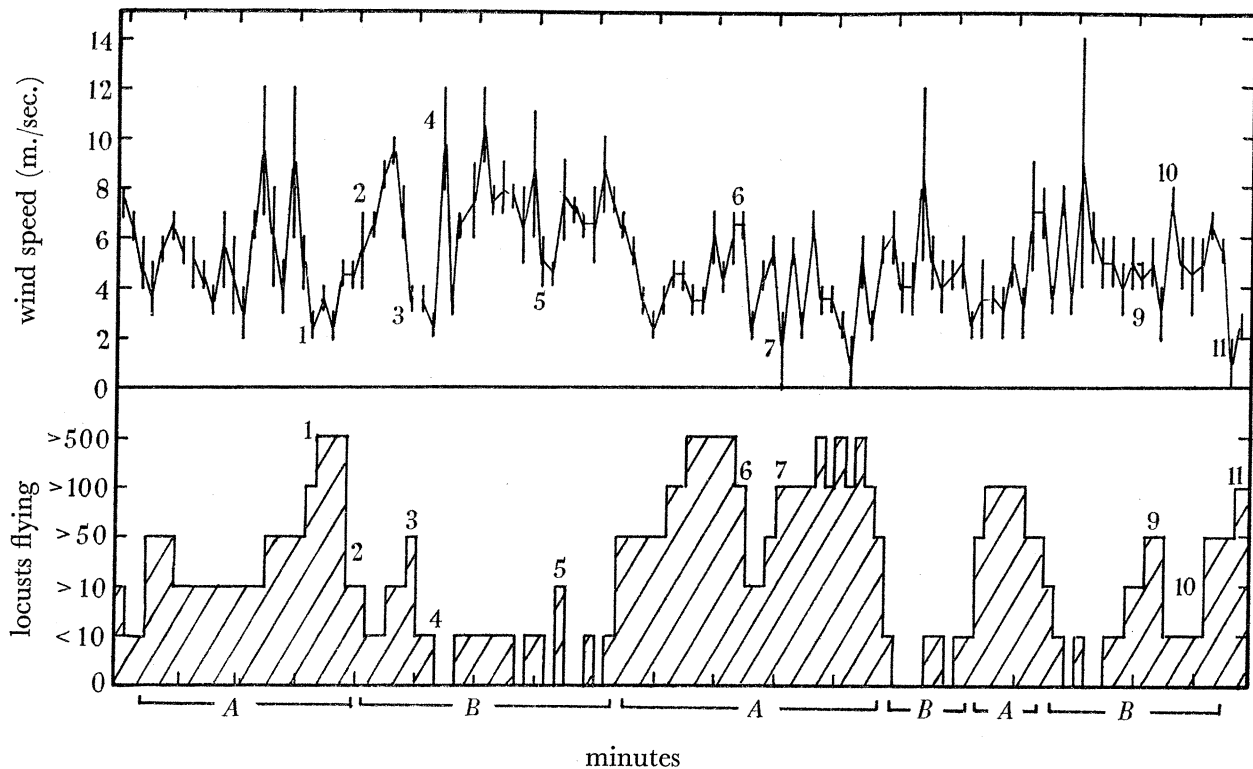


FIGURE 4. Wind speed and flight activity among fledglings. Instantaneous readings of wind speed, taken every 10 seconds with a swinging ball anemometer, and simultaneous rough estimates of the number of locusts flying in front of the observer. 09.10 to 09.29 hr., 13 June 1943. For lettering and numbering on figure, see text.

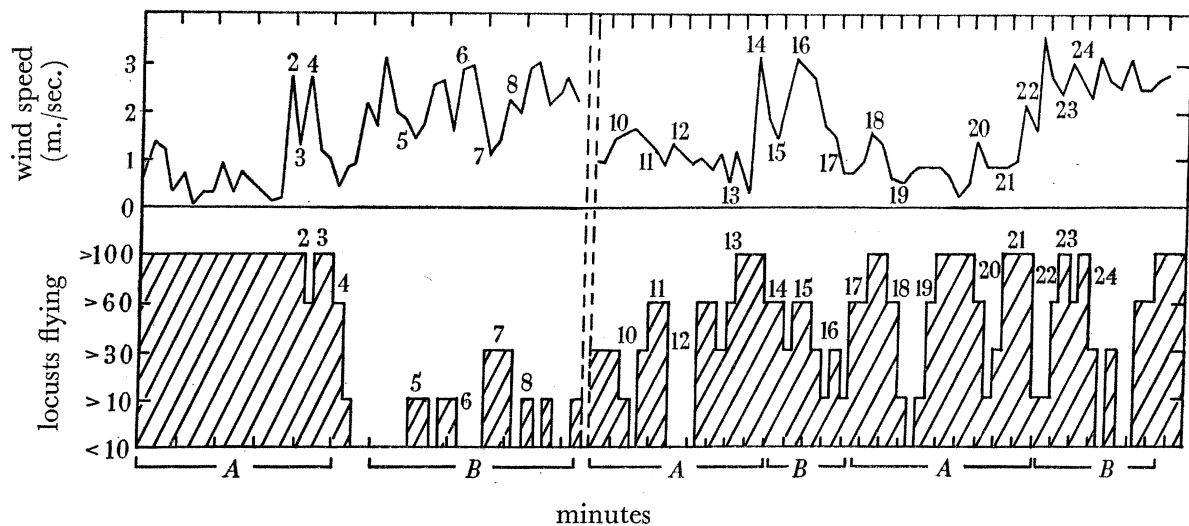


FIGURE 5. Wind speed and flight activity among fledglings. Mean wind speeds during the previous 15 sec. (up to the break in the record) or 30 sec. (after the break), taken from the readings of an integrating (windmill type) anemometer, and rough estimates made during the same periods of the number of locusts flying in front of the observer. 14.19 to 14.30 hr., 14 June 1943. For lettering and numbering on figure see text.

settled at once. Some, especially those rather higher in the air, were carried a little distance with the wind, turning as they went. Thus it sometimes happened that, after the onset of a gust, mass settling by the locusts in front of the observer was masked in his counts by the sudden appearance of a fresh group of locusts brought on the gust and destined to settle, if the gust persisted, beyond the narrow limits of the arc to which he confined his gaze for counting purposes.

Again, during brief, shallow lulls after the average wind speed had risen the locusts taking off from the ground in front of the observer were sometimes added to in the air by others surging temporarily forward again from beyond the observation area, thus exaggerating the effect of the momentary lull as a flight-evoker and masking the effect of the increased average wind speed as a flight-reducer. But, apart from these complications due to influxes of locusts from outside the observation zone, those in that zone seemed to respond even to very temporary changes of wind speed, over very different ranges of absolute wind speeds. This is reflected, although imperfectly, in figures 4 and 5.

Thus both the long- and short-term effects of wind on flight activity seemed to be effects of *changes* in the wind speed. A drop in wind speed led to an outburst of flying not only when the level to which the wind dropped was low, but also when it was quite high. This was often noted, and might mean that the wind excites the insects even while it temporarily suppresses their actual flight activity. That was the impression gained during some previous observations on non-gregarious locusts (Kennedy, in preparation) and strengthened by watching fledglings a few days before the above records were taken, on a day of pronounced gusts and lulls. When a gust came most fliers settled on the solid ground, but some settled on trees, etc., where they were exposed to direct buffeting by the wind as well as being shaken by the movements of their perches, such as palm leaves. These exposed locusts took off again in any momentary pause in the wind, or even without one, while the rest, secure on the ground, remained there until there was a good lull. Thus, both sets of locusts gave up flying when the wind increased, yet the ones that came to rest where there was more wind, took to flight again sooner. An extreme case, when the excitatory effect of wind became apparently completely dominant over its inhibitory effect, was observed at Jask on the Iranian coast during several days of April 1943 (table 2, nos. 6 and 10). Winds were then quite exceptionally violent and the locusts seen were almost all flying (see p. 183).

There is some further, if indirect, quantitative evidence on the flight-reducing effect of wind. All the occasions when migrants were observed, listed in table 2, have been retabulated in table 4 in terms of the height of flight and the ground (1.5 m.) wind speed which were typical or predominant on each occasion. On many occasions other combinations of height and wind speed were temporarily but commonly seen, especially when the wind was gusty. These further, 'frequently occurring' combinations are added to the 'predominant' ones to make up table 5. In both tables and in figure 6, where the data in table 5 are shown graphically, the percentage of high-fliers decreases and that of low-fliers increases as the wind speed increases. The height-reducing effect of stronger winds is reflected also by the absence from table 8 (p. 191) of any cases of semi-migrants flying higher than 8 m. in winds exceeding even 2 m./sec.

The quantitative records are, however, inadequate to support the stated conclusions on the effects of wind on the amount, height and speed of flight. The conclusions rest mainly on

impressions and it is desirable that more precise data should be obtained by better methods under a variety of conditions.

TABLE 4. HEIGHTS OF FLIGHT ACCORDING TO GROUND WIND SPEED. FULL MIGRANTS ONLY. DATA FOR PREDOMINANT BEHAVIOUR, FROM TABLE 2

wind speed (m./sec.)	frequencies		% low
	low (< 8 m.)	higher (> 8 m.)	
< 1	7	9	44
1- < 4	26	16	62
4 +	15	7	68

TABLE 5. HEIGHT OF FLIGHT ACCORDING TO GROUND WIND SPEED. FULL MIGRANTS ONLY. AMPLIFIED DATA INCLUDING FREQUENTLY OCCURRING AS WELL AS PREDOMINANT BEHAVIOUR

wind speed (m./sec.)	frequency distribution % by height of flight (m.)				no. obs.
	< 2	2-7	8-30	> 30	
< 1	25	29	26	20	72
1- < 4	32	39	24	5	73
4-7	39	33	18	10	49
no. obs.	60	65	46	23	194

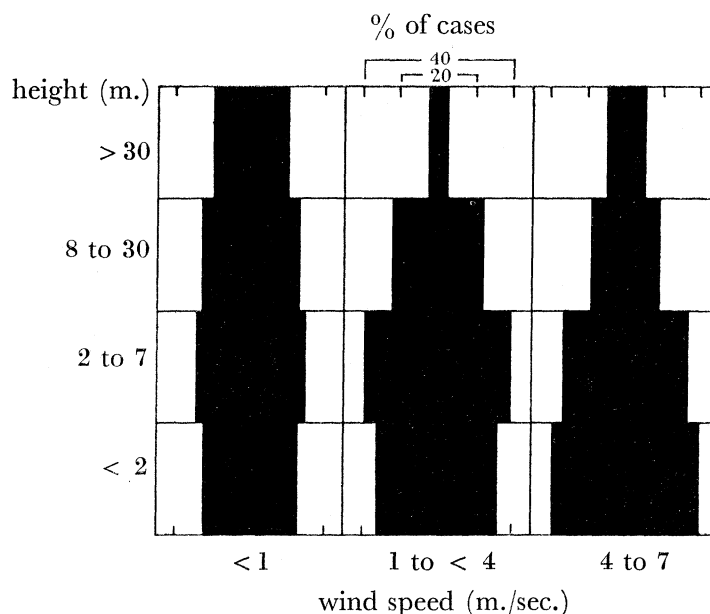


FIGURE 6. Frequency distributions of observed heights of flight among fully migrant swarms in different wind speeds. Data from table 5. Horizontal width of each block proportional to the percentage of records for that height range, out of the total for the indicated wind speed range.

Direction of flight. The majority of swarms observed were migrating roughly against the wind as can be seen from table 2 and the last line of table 6 (p. 190). The next most frequently observed direction was the opposite one, with the wind. The wind was, however, sometimes negligibly weak, and sometimes strong enough to interfere noticeably with the locusts' flight. It was obviously insufficient to record the relation between wind direction

and flight direction in the hope of finding regularities without at the same time noting the wind speed. Some incidents will serve to illustrate the effect of wind speed on direction.

On 11 April 1944 a swarm (nos. 16 and 17, table 2) was observed near Nakuru, Kenya, progressing slowly in dull weather against a 3 m./sec. wind from the south-east for about $1\frac{1}{2}$ hr. The wind increased suddenly to about 6 m./sec., without any other weather change, and the swarm was swept back with it and reoriented down-wind, covering 12 km. in at most 20 min. (10 m./sec., 23 m.p.h.) before it settled for the night.

In the spring there is typically a strong northward and north-westward trend of migration in Iran (Predtechensky 1935 *a*), and swarms were repeatedly observed (table 2) flying in that direction, roughly against the wind when its speed was moderate. Occasionally swarms were seen during short periods of stronger wind blowing from the same direction (table 2, nos. 24, 25 and 43), and these swarms were flying with the wind.

In March 1944, an extremely rapid movement of swarms took place across central and south-east Arabia, the Persian Gulf, south Iran and on into India. O. B. Lean (unpublished records at Anti-Locust Research Centre), then in south Iran, noted that the passage of these swarms coincided with a spell of exceptionally strong winds from the west. In the previous year a similar, very fast, eastward migration of young swarms took place, which cleared the coastal areas of western Iranian Mekran and led to the infestation of Pakistani Mekran. In that year, 1943, Messrs N. A. Janjua and A. G. Hussain were stationed at Jask and were able to watch the locusts actually leaving (table 2, nos. 6 to 10). They reported that a wind of gale force blew on 13 to 17 March from the west, that is, across the prevailing seasonal wind, and in the course of those days the area was entirely cleared of locusts. The locusts were seen being tossed and swept along, orientated down-wind and with their wings sometimes actually blown forward over their heads.

The *height* at which locusts were flying also seemed to influence their flight direction relative to the wind direction. Different flight directions were sometimes observed in the same swarm at different heights above the ground. The lower fliers in a swarm which met a strong wind near Lake Naivasha on 24 May 1944 have already been described (p. 178) as coming lower and continuing their up-wind progress, but at the same time the higher fliers were carried and turned down-wind and some eventually passed out over the lake again. Another swarm, about 2 km. in diameter (table 2, no 48), was watched over land to the east of Lake Elmenteita on 23 April 1944. Most of it was in a hollow bounded on the north-east by a steep slope. The bulk of the locusts were flying low against a wind from the north-east. As soon as they reached the top of the ridge the locusts encountered a stronger wind, lost headway, wheeled and were swept rapidly back with the wind. At times these recoiling locusts formed a definite stream with a common down-wind orientation; at others they formed only loose disorderly groups. In either case they sooner or later came lower, turned and rejoined the main stream moving up the slope below them. But the locusts moving down-wind extended far back over the main swarm so that there were two layers of locusts, a dense lower one flying up-wind and a thinner upper one drifting and sometimes oriented down-wind. More transiently and on a smaller scale the same arrangement of lower up-wind fliers and higher down-wind fliers was observed many times.

Winds are stronger higher up, away from the frictional drag of the ground, and down-wind flight might be expected to appear more often at greater heights on these grounds

alone. But there were occasions when higher fliers were moving about at random while lower fliers were moving either up-wind or down-wind, predominantly the latter. This was seen on 20 May 1943, 1 June 1943 and on 22 April 1944 (see p. 177), when the different behaviour of higher locusts could not be explained by the stronger wind aloft.

There were many other occasions when a swarm was watched for some time while the wind speed varied with evident effects on the locust's behaviour. The actual course of such behaviour changes could not be recorded in quantitative terms, but the following general account represents the observer's firm impression from all the observations. Without some such direct evidence of orientation reactions to wind, little value could be attached to the more quantitative but indirect evidence on the same subject which is quoted later.

For this account, the terms *course* and *track* are borrowed from navigational language, as was done by Gunn *et al.* (1948, p. 44), whose definitions may be repeated here:

'The *course* of a locust is the direction in which it is heading and in which its body is orientated; its speed relative to the air mass around it is its *airspeed*. The direction of its movement relative to the ground is called the *track* and the corresponding speed is the *ground speed*.'

The locusts were most commonly seen flying low and roughly against the wind. When its speed increased and they seemed to increase their air speed as already described (p. 177), they held tenaciously to their orientation, directly or more often slightly obliquely, into wind. In consequence their directions remained fairly steady and parallel as between locust and locust *as long as the wind remained moderate in speed*. When the wind speed reached 4 to 5 m./sec., however, the locusts' behaviour became noticeably erratic. Their directions varied from moment to moment and from locust to locust as gusts came and went, although tending always to return to the old direction, with the swarm as a whole progressing into and across wind by what Gunn *et al.* (1948, p. 15) have aptly termed a 'rolling' action.

Close attention to the behaviour of individuals under such strong-wind conditions led to the following conclusions about the detailed course of events. The locusts did not always increase their air speed sufficiently, or sufficiently quickly, when hit by a gust, to prevent themselves being carried backwards. But they were never seen to be carried backwards for more than a moment, for at such wind speeds, before or after backward carriage had occurred detectably, they either settled (p. 178) or turned away from their up-wind orientation, toward the same side as their track had already been deviated from that course by the wind. It was as if they were pursuing their own runaway tracks.

Locusts which thus turned away from the up-wind orientation did not always turn right round and fly due down-wind. They often stopped turning when they had attained an orientation in which there was at least no backward component in their movement over the ground, although there was a greater or lesser degree of sideways drift. Consideration of the vector quantities involved shows that by turning aside in this way, the locusts reduced the chances of gusts introducing a backward component into their movement relative to the ground, even without further increase of air speed on their part; and, having so turned, the increase of air speed required to eliminate any backward component imposed by a gust was smaller than that required while oriented directly into the wind.

The deviated locusts sometimes continued on a cross-wind course, until the wind slackened again, whereupon they reverted to an up-wind course. The cross-wind orientation seemed to

be relatively unstable and transient, however, for if the wind did not drop and allow the locusts to turn up-wind again, they commonly continued the down-wind turn and took up a due down-wind course. If after this the wind still did not slacken they apparently came down and settled. Fliers were always seen to turn into the wind just before alighting, even if they were not so oriented previously.

Higher fliers showed the same general behaviour pattern as lower ones, but it was distinctly more 'ragged'. They were thrown into greater confusion when hit by a gust than lower fliers hit by the same gust, resisted being drifted backwards less tenaciously and turned down-wind less quickly when being carried backwards. After a gust had passed, higher fliers did not return to up-wind orientation as rapidly as lower fliers. Since, in spite of the fact that wind speeds are greater aloft, away from the frictional drag of the ground, higher fliers were nevertheless less responsive than lower ones when hit by the same gust, it was concluded that markedly stronger winds were required to evoke responses from the higher fliers.

The behaviour of fledgling and sexually active locusts, classified as 'semi-migrants' (p. 173), in wind, was in principle the same as that of full migrants, with the important difference that the wind speed causing them to lose headway, turn down-wind and settle was decidedly lower than for full migrants.

The same general pattern of behaviour in wind, whether of full migrants or semi-migrants, was characteristic of single, isolated fliers and not merely of dense swarms. There were some differences between scattered and dense swarms, which will be dealt with under 'gregariousness'.

Although no more precise method was available for recording the actual progress of the locusts' responses described impressionistically above, a method was devised for obtaining more quantitative 'snapshot' data on the course, track and height of selected individuals at given moments, with simultaneous readings of the wind direction and speed. It was impossible for one man to record all these items simultaneously, and it proved inaccurate and exhausting to read course and track by looking up at the locusts and then down at a compass. The method used required three persons. One recorded the readings called out to him by the other two, of whom one watched the anemometer, calling out the wind speed and direction at once every time the third man called out his readings of locust directions. The anemometer was of the swinging-plate type, an Italian model having a light aluminium sphere instead of a plate and giving instantaneous values for wind speed and direction at 1.5 m. above the ground. Throughout the present account, contrary to the conventional practice followed by Gunn *et al.* (1948), the direction given for the wind is that *toward* which it was blowing, so as to conform with the way of giving locust directions.

The third man took readings on what may be called the 'flight direction-finder' (figure 7). This consisted of a plate glass mirror 35 cm. square laid face upwards on a suitable support. In the centre of the mirror a spindle was fixed and on it was pivoted a horizontal grid of wires. The centre wire was elongated so that its tip passed over a scale of degrees marked on the mirror. Having first oriented the mirror with respect to the compass, the observer had only to pick out a particular locust seen passing across the mirror, quickly set the grid so that the wires lay parallel first with the course and then with the track of the locust, and call out the readings obtained. It would have been an advantage to have had a small swivelling telescope attached to the apparatus for readings from high-fliers.

Before considering the whole collection of separate records of flight direction in relation to wind speed and height, a few series of records taken from single swarms may be quoted. These merely supplement, and cannot fully take the place of the impressions formed at the time, so that the two must be given together. But these disconnected 'snapshot' records may be taken as partially illustrating what has been described above as the general impression, and as showing the possibilities of a method which requires further elaboration before it can be used to provide quantitative information on the continuous *process* the observer sees.

Figure 8 shows four sets of records from full migrants between Anar and Kerman, Iran, on 20 to 22 May 1943. The course and track of each individual, the direction toward which the wind was blowing and the wind speed at the same moment, are all entered at the same point along the horizontal time axis, that is, in one vertical row. Readings were taken in

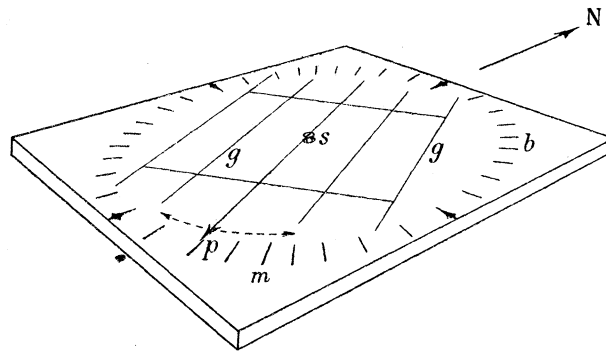


FIGURE 7. Diagram of the 'flight direction-finder'. *m*, mirror, oriented with reference to the compass; *s*, spindle bearing *g*, rotatable grid of wires of which the centre one projects to form a pointer *p*, moving over the scale of bearings *b*, marked on the mirror at 10° intervals.

the order shown, but not quite at the regular time intervals shown. The successive readings are connected up merely to guide the eye, having been taken from different individuals. It is emphasized that the records were not taken at random, individuals being selected with a bias toward those temporarily deviated from the predominant direction, and toward moments when the wind was exceptionally strong.

In series *A* (44 min. duration) the wind was weak, usually 0 to 2 m./sec., and usually blowing to 120° but variable in direction. The locusts were flying almost exactly against the mean wind direction, and even those selected for recording nearly all kept their courses steady, sudden wind accelerations or direction changes causing only sporadic deviations of track from course.

In series *B* (24 min.) the wind was stronger than in *A*, usually 1 to 3 m./sec., but steadier in direction. The locusts were flying slightly to the left of due up-wind most of the time, and again even selected ones kept their courses nearly steady, but their tracks were often temporarily deviated by changes of wind speed and direction.

In series *C* (24 min.) the wind was generally higher and steadier in speed than in *B*, about 3 m./sec., but made a marked directional diversion away from its normal, and back again, during the period when the readings were taken. Most of the locusts were flying somewhat to the left of directly against the normal wind direction, but their courses were rather

more variable than in series *B*. These variations were smaller, however, than the changes in wind direction, and the locusts' tracks were not always and not greatly different from their courses.

In series *D* (24 min.) the wind was stronger even than in *C*, 3 to 7 m./sec., although steadier in direction. On the average, the locusts were flying slightly to the right of due up-wind, but their courses here changed with changes in the wind and their tracks were nearly always deviated from their courses.

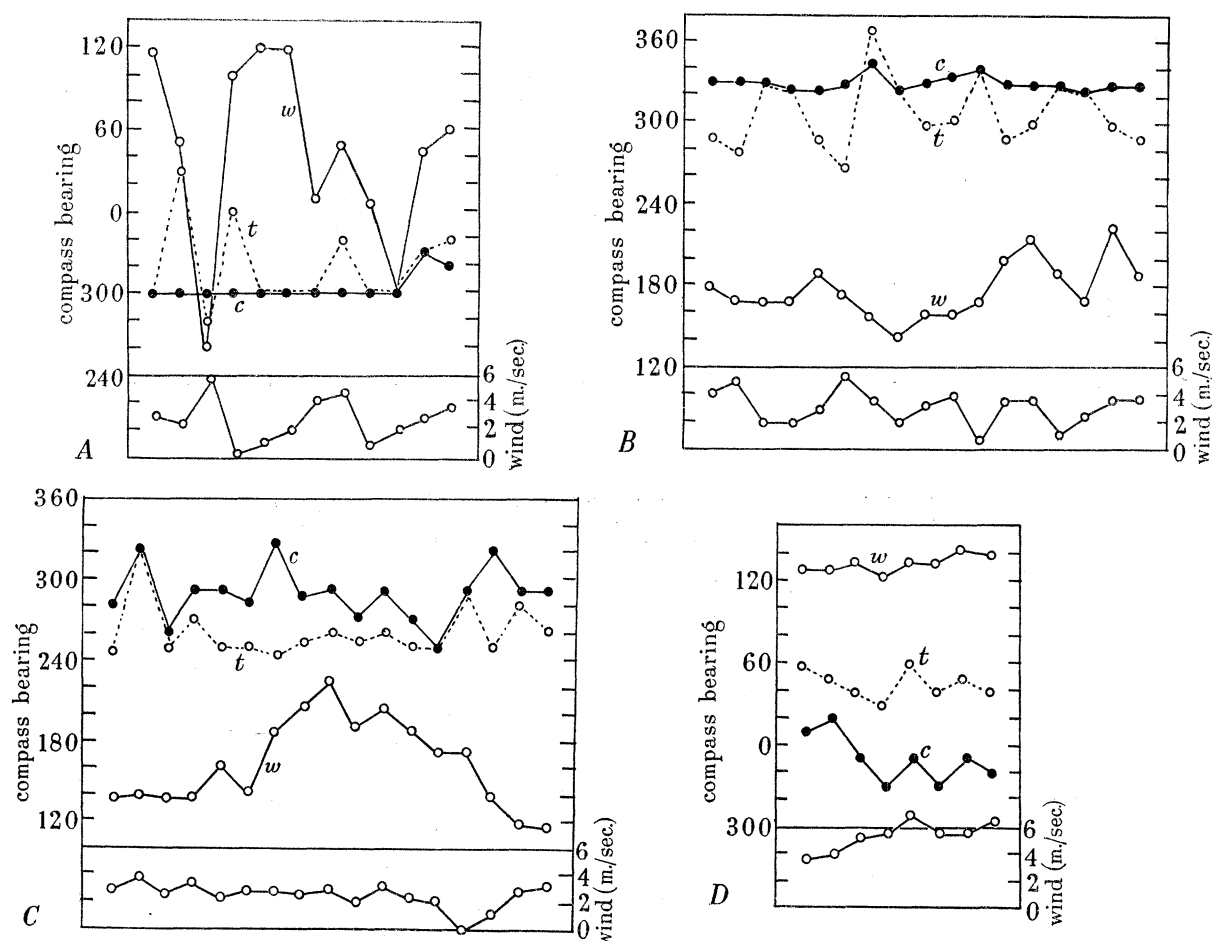


FIGURE 8. Individual direction-readings from successions of locusts flying at 1 to 4 m. above the ground in swarms migrating roughly against the wind in full sun. *c*, course of locust; *t*, track of locust; *w*, direction toward which wind was blowing. For further explanation see text, p. 186.

To sum up, the locusts adhered firmly to their set courses roughly against the mean wind direction, despite deviations of track when the wind accelerated, unless the wind speed exceeded 4 m./sec., when their courses became distinctly erratic.

The readings taken from full migrants do not include any examples of their turning right round and flying with the wind, although this was not infrequently seen, especially among higher fliers. Such complete reversals were observed more often among fledglings, because they were thrown into confusion by the more commonly experienced, weaker winds against which full migrants made steady headway. Readings taken with the flight direction-finder from fledgling swarms in the region south of Bam, south-east Iran, are shown in figures 9 and 10.

The swarm from which the readings shown in figure 9 were taken consisted of advanced fledglings making very slow, rolling progress against the wind through an open tamarisk grove on 16 June 1943. Flocks of the locusts took off and surged forward whenever the wind

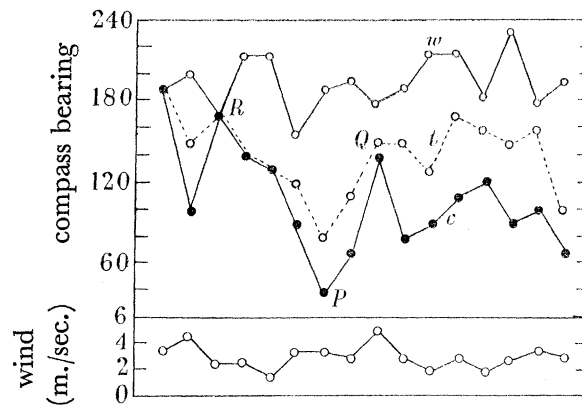


FIGURE 9. Individual direction readings from fledgling locusts flying within 3 m. of the ground and deviated from their initially up-wind tracks by the wind. Constructed as figure 8.

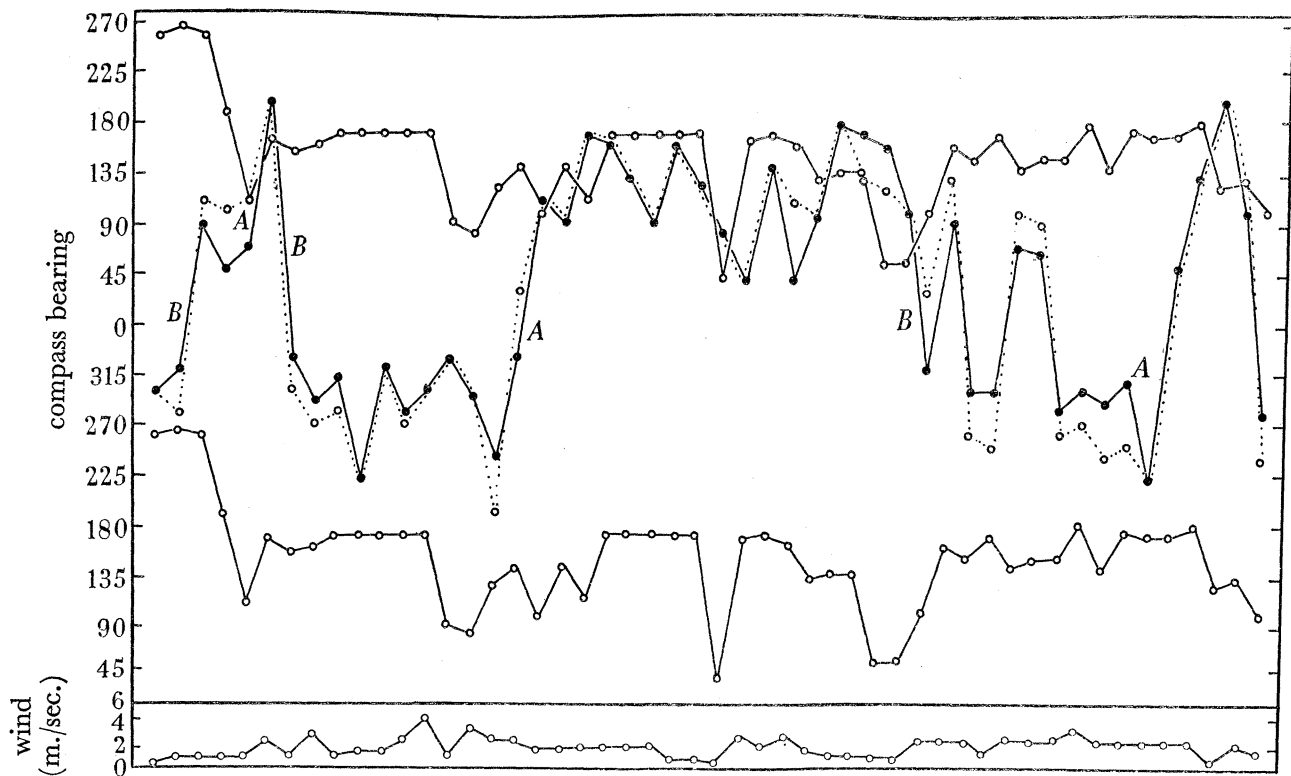


FIGURE 10. Individual direction readings from fledgling locusts flying 2 to 6 m. above trees, with periods of roughly up-wind flying alternating with periods of down-wind flying. Constructed as figures 8 and 9, but direction axis extended so that the wind direction (toward which it was blowing) appears twice, to make clear the relation between locust and wind directions.
—•—, course of locusts; ···○···, track of locusts; —○—, wind.

dropped, but most of the time the wind speed was over 2 m./sec. and the great majority of the locusts were grounded. Those that took off then did so into wind, but were immediately deviated on to cross-wind tracks and reoriented themselves accordingly, as described on

p. 184, in such a way that backward drift was as a rule prevented. It was from these *disoriented* individuals that the readings were taken, which did not therefore represent level, steady courses and tracks. Very few of these individuals managed to hold even an approximately up-wind course (*P*), and some turned nearly (*Q*) or completely (*R*) round on to a down-wind course. These flights were all brief, for the fliers soon came down and reoriented into wind close to the ground or settled again.

The behaviour of fledglings not in a position to reach the ground so quickly, because they were higher up when the wind became too strong for them, was recorded on 12 June 1943 (figure 10). The recorded fliers were at 2 to 6 m. above the trees of an oasis. The tracks of lower fliers (not recorded), in calmer air, seldom diverged from their courses which were slightly to the left of due up-wind. But the tracks of the higher fliers, exposed to stronger winds, frequently diverged from their courses. For varying periods, nearly all the higher fliers would be facing and flying roughly up-wind like the lower fliers, but then they began to waver, their tracks diverged from their courses and they then turned right round and flew roughly down-wind. The more frequent occurrence of down-wind courses and tracks among these fliers, than among those closer to the ground at the same time or those recorded in figure 9, seemed to be due directly to their greater distance from the ground. They were exposed to stronger winds and, taking longer to come down and settle, they were exposed for longer to winds against which they could not make steady headway, so that the reorientation response received fuller expression. In figure 10, it will be seen that the readings fall into two groups, either roughly up-wind or roughly down-wind, with switching from up- to down-wind (*AA*) and vice versa (*BB*). The switchings are not obviously correlated with changes in the wind speed in the figure, for the anemometer was below the level of the locusts and somewhat sheltered by trees. The wind-speed changes to which the high-fliers were exposed could often be inferred from the waving of foliage and the momentary quickening or slowing of the fliers' ground speed, and it appeared that switches from up- to down-wind followed sharp gusts and switches from down- to up-wind occurred in lulls. However, the occurrence or non-occurrence of such a switch appeared to depend not only on wind-speed changes, but also on the density of the fliers (gregariousness, see p. 194).

We may now consider the records of flight direction in relation to wind, collected from all the swarms observed. Numerically, these constitute more substantial evidence than any so far quoted, but are given last because they are not direct evidence of the wind *responses* discussed above. If, however, such responses are real and important, then we might expect them to be reflected in the frequencies at which different courses and tracks appear at different heights and wind speeds.

The predominant relation between flight direction (course) and wind direction on each occasion when full migrants were seen has been taken from table 2 and entered in table 6 according to the height of flight and the wind speed prevailing near the ground (at 1.5 m.). There were a total of forty-six occasions when both wind and swarm had a definite direction. The bottom line of table 6 shows that, among these, the swarms were flying roughly up-wind on thirty and down-wind on nine occasions. Flights at 45 to 90° from due down-wind occurred on three and at 90 to 135° on four occasions.

In the main body of the table, where the observations are classified by height of flight, the totals are smaller because not all the swarms extended both above and below 8 m. The

number of down-wind flights below 8 m. was equal to the number over 8 m. (seven swarms extending to both levels). The number of up-wind flights below 8 m. was, however, nearly twice the number over 8 m. (eleven swarms extending to both levels). At both heights all but one of the eight cases of down-wind flight occurred with winds at 4 or more m./sec., and

TABLE 6. COURSES OF FLIGHT IN RELATION TO WIND DIRECTION, ACCORDING TO GROUND WIND SPEED AND HEIGHT. FULL MIGRANTS ONLY. DATA FOR PREDOMINANT BEHAVIOUR, FROM TABLE 2.

height of flight (m.)	wind speed (m./sec.)	frequency distribution by angle from due down-wind (0°) (actual numbers)				totals
		0-45	45-90	90-135	135-180	
< 8	< 1	0	2	2	1	5
	1-<4	1	0	2	21	24
	4+	7	0	1	5	13
	total	8	2	5	27	42
> 8	< 1	0	2	0	2	4
	1-<4	1	0	1	12	14
	4+	7	0	0	0	7
	total	8	2	1	14	25
total swarms		9	3	4	30	46

TABLE 7. COURSES AND TRACKS OF FLIGHT IN RELATION TO WIND DIRECTION, ACCORDING TO GROUND WIND SPEED AND HEIGHT. FULL MIGRANTS ONLY. AMPLIFIED DATA INCLUDING FREQUENTLY OCCURRING AS WELL AS PREDOMINANT BEHAVIOUR.

height of flight (m.)	wind speed (m./sec.)	course or track	frequency distribution % by angle from due down-wind (0°)				no. obs.
			0-45	45-90	90-135	135-180	
< 8	< 1	C	4	22	22	52	23
		T	4	22	22	52	
	1-<4	C	6	9	13	72	46
		T	14	17	15	54	
	4-7	C	28	18	23	31	39
		T	52	15	13	20	
> 8	< 1	C	8	25	21	46	24
		T	8	25	21	46	
	1-<4	C	12	16	12	60	25
		T	20	28	12	40	
	4-7	C	57	15	14	14	14
		T	72	10	9	9	

five of these cases occurred during winds of gale strength (nos. 6-10, table 2). At both heights the majority of up-wind flights occurred in winds of 1 to <4 m./sec., but while there were five up-wind cases in stronger winds below 8 m., there were no up-wind cases in such winds above 8 m.

The total number of cases is small if only predominant directions are taken into account as above. These are therefore supplemented, in table 7, by a selection of the 'snapshot' readings taken during the more extended observations on single swarms. Many of the readings obtained during such detailed studies represented temporary conditions diverging more or less from the predominant one at the time. Although only the predominant direction represented the effective direction of migration at the time, the supplementary data can

be used legitimately for the study of behaviour. Only those relations between wind and flight which occurred especially frequently among the assortment of relations noted during any one swarm study have been selected for inclusion, together with the predominant relations at the same time, in table 7. The same figures are presented graphically in figure 11. Figures for semi-migrants, arrived at in the same way, are presented in table 8 and figure 12.

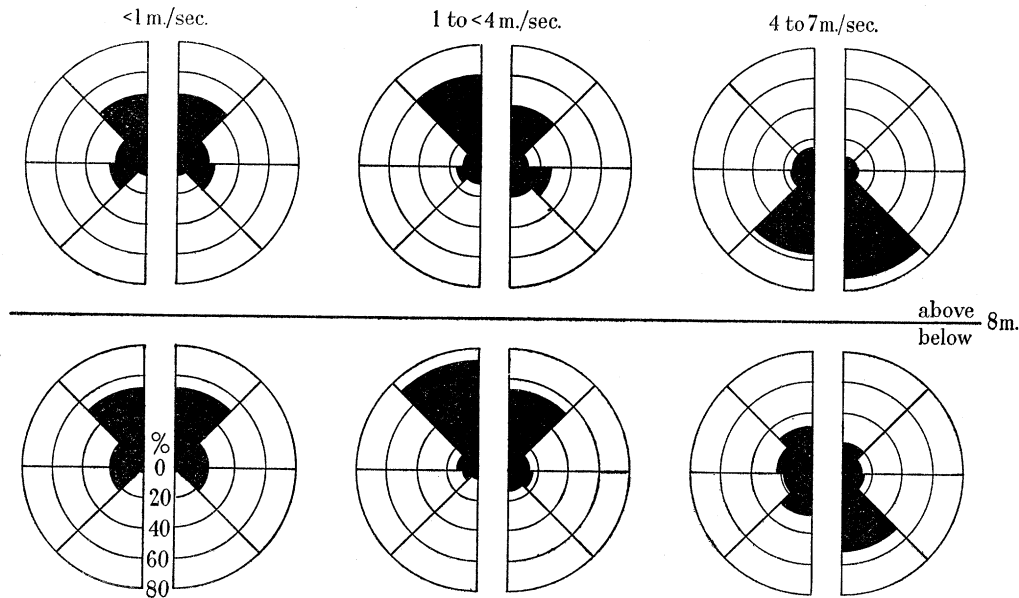


FIGURE 11. Frequency distributions of observed directions of flight of fully migrant locusts, according to height and wind speed. Wind is assumed to be blowing from the top of the page. Locust courses are shown in the left half, and tracks in the right half of each of the six diagrams. Each half diagram is divided into four sectors representing courses or tracks deviating by 0 to 45°, 45 to 90, 90 to 135 and 135 to 180°, from due up-wind. Deviations of course to both left and right are shown together as deviations to the left, and deviations of track to both left and right are shown together as deviations to the right; the particular side toward which the deviations occurred being immaterial here. Within each of the four sectors a portion is blacked-in with a radius equal (on the scale shown in the bottom left diagram) to the percentage of records within that range of deviations. Data from table 7.

TABLE 8. COURSES AND TRACKS OF FLIGHT IN RELATION TO WIND DIRECTION, ACCORDING TO GROUND WIND SPEED AND HEIGHT. SEMI-MIGRANTS. AMPLIFIED DATA INCLUDING PRE-DOMINANT AND FREQUENTLY OCCURRING BEHAVIOUR.

height of flight (m.)	wind speed (m./sec.)	course or track	frequency distribution % by angle from due down-wind (0°)				no. obs.
			0-45	45-90	90-135	135-180	
< 8	< 1	C	19	19	12	50	16
		T	19	19	12	50	
	1-4	C	28	19	17	36	59
		T	34	22	15	29	
> 8	< 2	C	31	23	15	31	13
		T	31	23	23	23	

For what they are worth, the figures clearly fit the conclusions drawn from the continuous observations of single swarms. The reversal from preponderantly up-wind to preponderantly down-wind orientations, when the wind exceeds 4 m./sec., reflects the direct

observations of such reversal occurring when the locusts ceased to make direct headway against such winds. The figures bring out a further point, that across-wind orientations were rare except in light winds. The lower proportion of up-wind courses among higher than among lower fliers, reflects the direct observation of the lesser responsiveness of higher fliers. In winds of 4 or more m./sec. there is a lower proportion of down-wind courses among lower than among higher fliers, which reflects the direct observation that the response of turning down-wind, although not so readily initiated among higher fliers, was nevertheless more often carried to completion and the new orientation maintained than among lower fliers which were able to settle or resumed up-wind flight instead.

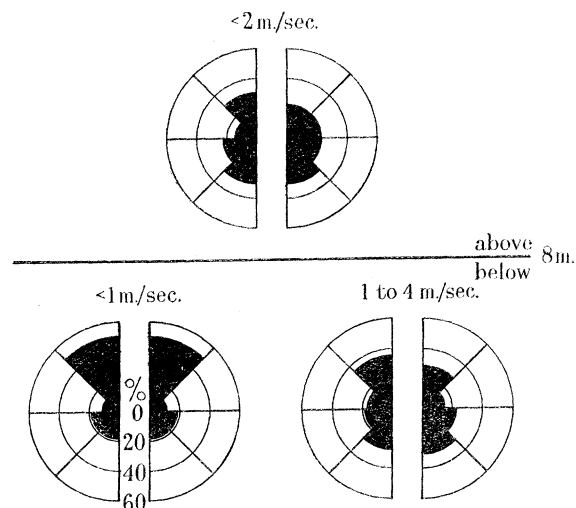


FIGURE 12. Frequency distributions of observed directions of flight among semi-migrant locusts, according to height and wind speed. Constructed as figure 10. Data from table 8.

The numerical data for semi-migrants (figure 12) present a picture similar to that for full migrants, except that the change-over from up-wind to down-wind orientation occurs at a lower wind speed, corresponding with the observed weakness of the flight of semi-migrants.

To sum up, the body orientation of low-fliers was across the wind ($90 \pm 45^\circ$) in only a minority of cases. The minority was considerable, but it was smaller in moderate than in light winds. In the majority of cases the orientation was against the wind, or with it when the wind became too strong, and the wind strength which was too great depended on whether the locusts were full migrants or not. But once again it is very desirable that more and more precise data be obtained on these questions.

Behaviour over water. The effect of wind on swarms flying over water was observed twice, on 23 and 24 May 1944, at Lake Naivasha, Kenya. These observations are treated separately here because behaviour over water differed from behaviour over land in material respects. The behaviour of part of the swarm observed on 24 April 1944 has already been described; that part which had already left the lake and passed on over the shore and came down when the wind speed increased. The remarkable point was that the part of the swarm that was still over the water when the wind strengthened, did not come lower. The same applied to higher flying locusts that had advanced only a little distance over the land when the wind increased, and were blown back over the water before they had time to drop down among the trees. These two sets of locusts remained at the same height and were carried down-wind

although still facing up-wind, while their fellows over the land had not lost ground but dropped low among the trees.

The same effect was observed on the previous day when a large pink swarm made repeated sorties from the northern shore of the western arm of the lake, heading south against the wind. The swarm was observed through field-glasses from the opposite shore. The following sequence of events was repeated five times. At the end of a spell of strong wind, 5 to 8 m./sec. (as recorded on open, raised ground), the locusts had disappeared from view on the land, where they had settled or were flying too low to be seen. The wind speed then dropped to 2 to 5 m./sec., and in a minute or two the locusts rose into view, flying steadily against the wind and in increasing number, and moved out over the lake. Over the land they remained relatively low, not exceeding 15 or at most 30 m., but as they advanced over the water they deployed upwards to 100 or more metres. Sometimes they advanced as much as 1 km. over the water in this way, sometimes much less, before the wind rose again and drove them back. Each time this happened they drifted back in disorder and without losing height as long as they were over the water; in contrast with swarms driven back by gusts over land which soon regained their cohesion by turning *en masse* down-wind, and came lower. As soon as the lake swarms reached the land, however, they became more orderly, began to lose height rapidly and, if the wind did not drop in a few minutes, they all dropped down out of sight.

These were the only occasions when locusts were seen to offer no resistance to being carried backwards by the wind. On both occasions they were over a considerable sheet of water, which suggests that the failure of the normal behaviour was due to the uniformity of the visual field below.

Gregariousness

The term *gregariousness* is used here in the strictly behavioural sense, meaning the tendency of swarm members to act in certain ways because other locusts are doing so and not because all are responding to a separate, common source of stimulation.

Flight activity. The flight-engendering effect of mutual stimulation was evident during the process of increasing flight activity culminating in mass departure, as already described. From the start of *milling* onwards it was noticeable that taking-off was flaring up and dying down again among whole groups of locusts, now at one series of points and again in a different series of points in the swarm. Taking-off, started by a few individuals, would run through the cluster along a tree branch like a flame. Meanwhile neighbouring clusters remained perfectly quiet, until for some reason a few of their members took off, and the activity spread through fresh masses of insects. Groups of flying locusts flushed up resting ones from trees and from the ground. *Milling* passed into *surging* as the groups enlarged, gregariousness and rising temperature apparently collaborating in bringing more and more insects into the air together.

The flushing up of settled locusts by flying ones passing over them reached a climax in the mass departure of the swarm. Up to mass departure there were still large numbers of settled locusts beside those flying. Within quite a short time—15 min. or so in our observations (figure 1)—they were all in the air, having risen in a succession of clouds from this point and that, as their fellows swept over them with the setting in of uninterrupted flying.

However, it was always noticed that the locusts which took off early, when flights covered only a few metres, did so individually, without appearing to affect their neighbours (cp. Gunn *et al.*, 1948, p. 14). Moreover, the trickling departures of semi-migrant mating and laying swarms consisted of innumerable takings to flight by individuals, again not apparently stimulated by their neighbours. And later in the day, when swarms were migrating, full migrants were often seen flying alone. In Iran, in May 1943, migrants were seen in very loose flights or as completely isolated individuals more often than they were seen in coherent swarms. Individual migration was also seen in Kenya in 1944, although less frequently. It was not known whether these migrants were already isolated when they started flying, or started in a swarm and became isolated later.

Thus although mutual stimulation appears to contribute to flight activity, both taking off and sustained flight can occur when mutual stimulation is relatively weak or even absent.

Flight direction. The term *gregarious inertia* has been applied to the tendency of a locust hopper band to continue moving in a straight line, thanks to the responses of hopper to hopper (Kennedy 1945). This effect was evident also in flying swarms, and most strikingly so when two columns of locusts met at an angle, as observed among maturing locusts in Kenya and several times among fledglings in Iran. The result has been described by Zolotarevsky (1929, 1930); the locusts from one swarm change their direction to that of the other according to which swarm is the denser at that point and time.

The case observed in Kenya, at Nakuru, on 31 March 1944 was a variant on Zolotarevsky's. Column *A* was flying east and denser in its upper layers than below, when it met column *B*, which was flying at the same height and was as deep as *A*, but was flying south-east and denser below than above. At the point of mixture most fliers in the upper part of *B* joined column *A*, whereas most in the lower part of *A* joined *B*. Where the columns were denser, in the upper part of *A* and the lower part of *B*, the locusts remained largely undeflected. Cases of locusts reorienting each other in this way attract most attention when they occur in full flight, but exactly the same thing can be seen again and again in a swarm surging about prior to the mass departure from the night roosting site. Indeed, the mass behaviour pattern leading up to the mass departure of swarms in the morning is one long display of direction changes mediated by gregariousness, or *gregarious re-alinement*. The essential principle of gregarious re-alinement remains the same throughout the process. What changes progressively is the number of insects involved in each re-alinement manoeuvre. The roles of provoker and executor of a gregarious re-alinement are filled at first by single insects, and then by ever-growing groups of them together until finally there is only one group, the whole swarm at mass departure.

Gregarious re-alinement was also seen in swarms in the course of migration during the day, under the influence of wind, and the difference between loose and dense swarms in this respect provided additional evidence of the role of gregariousness in regulating flight direction. The effects of wind, described in the previous section, were essentially similar in loose and dense swarms. But when the locusts were dense, their responses were more definite and less ragged than when they were thin. Dense locusts seemed less easily driven back and deflected. As long as the majority managed to make headway, deflected individuals came back into line quickly. On the other hand, as soon as a considerable proportion of the individuals began to be deflected and so to turn, the whole part or layer of the swarm

reversed its direction with remarkable rapidity. This phenomenon had a clear gregarious component. It was noticed in both migrants and fledglings; more often in the latter (e.g. figure 10), because the customary moderate wind was able to initiate a down-wind turn in these feeble fliers more readily than in migrants proper.

The following impression was formed of what happened during gregarious reversal. A mass of individuals was flying against the wind, which then increased in strength. Some individuals began to lose ground and turn away from their up-wind course. In consequence they began immediately to drop backwards relatively to their fellows. The immediate neighbours responded to this relative displacement by themselves turning and pursuing the deflected individuals, so that the neighbours assumed a due down-wind course even sooner than the initially deflected locusts. The result was to accelerate and fix a due down-wind course throughout the swarm whenever it became difficult for many individuals to make headway directly against the wind, but before it had become impossible for them all to do so.

The return of dense low-fliers to an up-wind orientation when the wind dropped again was seen to be accelerated in the same manner. As soon as a number of individuals had regained their up-wind course the others quickly followed suit. In the upper layer of loose swarms the reversal from up- to down-wind orientation was relatively slow and ragged. Where higher fliers were dense, and hit by a wind gust, the temporary confusion was more marked than among low-fliers, but then the rapid, unanimous reversal to down-wind was at least as conspicuous as in dense low-fliers. Mass reversal of higher fliers (> 8 m.) was also observed when low-fliers were maintaining their up-wind course and managing to make some headway. Thus gregarious reversal is merely a special case of direction changes mediated by gregariousness, or gregarious re-alignment, in circumstances where all except two, opposite directions are excluded by another factor, wind.*

Despite the above observations suggesting that gregariousness participates in direction determination, it should be emphasized that mutual stimulation is not essential for steady uni-directional and parallel movement by a large number of individuals. In Iran on 20 May 1943, for example, the average density of a passing swarm was estimated as one individual every 10 m., and some individuals were hundreds of metres from their nearest fellows. Yet all the individuals were flying steadily on the same course. Also, during the departure of both fully migrant and semi-migrant swarms, the assumption of a common flight direction was observed to occur among individuals completely cut off, at least visually, from their fellows (p. 172).

* Gregarious reversal can be seen in swarms of other insects. The writer observed it, for example, in a large swarm of male Chironomids stretching 10 m. along the centre of a narrow road bounded by high hedges near Salisbury, Wiltshire, in 1945. The midges were dancing 2 to 5 m. above the road surface, directing themselves into the light air drift along the road. Whenever the wind freshened, two things happened. The whole swarm shifted to a lower, more sheltered level, and mass down-wind turns occurred wherever the midges began to be carried backwards over the ground. At times a fast-moving *wave* of gregarious reversal was seen to pass back along the swarm, as down-wind fliers passed successive lots of the other midges, till then still facing up-wind and keeping their position with reference to the ground, but which now joined the down-wind surge. The down-wind movement occurred most commonly in the upper, more exposed layers of the swarm, producing the situation often seen among locusts and butterflies, the upper layers of the swarm oriented down-wind and the lower layers oriented up-wind. As soon as the wind dropped again, all the midges soon resumed their up-wind orientation, moved higher into the air and kept their rough position with reference to the ground despite moments of chaos caused by passing vehicles or the human voice.

The sun as a directing influence

Considered as a whole the records show no consistent relation between flight direction and the sun's position. There was no evidence that swarms kept the same orientation to the sun throughout a day's migration, for this would have meant flying in a large semi-circle, the evening direction being opposite to the morning one, and there was no sign of such a diurnal shift. In Iran there was a consistent trend northwards whatever the sun's position. In Kenya there was little consistency at all with relation to the compass or the sun. The relationship between flight and wind directions was far more consistent than between flight and sun directions. Nor was there any evidence that the direction of the whole day's migration might be derived from the basking orientation before mass departure in the morning, of which there are indications from hopper behaviour (Kennedy 1945).

That is not to say the sun played no part. The observations described above under 'wind' suggested that the locusts oriented on the wind and changed their orientation when it became too strong. It would seem to follow that changes in the wind's *direction*, at any rate if they were big and lasting, would also cause the locusts to change their orientation, although we were not fortunate enough to be present when such wind shifts occurred. But small, temporary wind changes occurred while a number of swarms were under continuous observation, and the striking feature of the locusts' behaviour then was the *steadiness* of their courses. The locusts did not follow every small shift the wind was making, but tended to remain oriented toward one point of the compass approximating to the mean wind direction. Quite large wind shifts often failed to change the locusts' orientation, when they lasted only a few minutes, the wind was not too strong and the locusts were flying at 5 or more metres. For example, on 21 April 1944 a flying swarm was seen extending from ground level up to 15 m., orientated directly away from the sun and directly against a 2 m./sec. wind from the south-east. The swarm rose gradually until its base was at 15 to 30 m. After 10 min. the wind direction changed to east-north-east, but the locusts retained their orientation with reference to the ground and sun.

The same stability of orientation is illustrated by the records obtained with the flight-direction finder (figure 7) in Iran, some of which are shown in figure 8, *A* to *C*, and discussed on p. 186. If orientation depended upon responses only to the wind, it would be expected that the locusts would change their orientation with every change of wind direction. Since they did not do so, but showed instead an impressive degree of stability of orientation, it appeared that they must have been responding also to some other environmental feature, which was less variable than the wind. The only obvious feature of that kind was the sun.

On 15 June 1943 a large plane mirror was used in an attempt to change the sun's position artificially. A loose swarm of young locusts was flying at 5 to 10 m. above the ground against a 1 m./sec. wind through an open grove of large tamarisk trees. The sun was in the west (about 280°) at an elevation of about 25° , and the locusts had it on their left sides as they flew slightly west of due north. Attempts were made to catch single locusts in the light of the sun reflected by the mirror on to their right sides, during the few moments they were passing through the shadow of a tree. It was possible to do this with only five individuals. On receiving the sun's image suddenly on their right sides, these locusts all swerved round instantly and flew in diametrically the opposite direction, losing height as they did so. They

did not maintain this orientation for more than a moment, for by then they were already free of the reflected light from the mirror and out of the tree's shadow. Three of them were lost sight of at once. The two that were kept in sight quickly reverted to their old direction. A further fifteen locusts were caught in the light of the mirror when they were not shaded from the real sun; they also swerved instantly but did not turn right round, and recovered their old orientation again almost at once. They remained in sight but it was again impossible to keep the mirror-light on them when they swerved.

Taken by themselves these mirror effects might be classed as mere shock-effects due to the sudden flash of reflected sunlight. Taken together with the observations on the notable stability of orientation described above, and in view of the results obtained by the same method with hoppers (Kennedy 1945), they provide some indication that the orientation of flying migrants may also depend partly on a light-compass-reaction to the sun.

Further evidence of the locusts' direction-stabilizing tendency was obtained during numerous attempts to throw individual migrants off their set course by chasing them. Practically always they reverted to their previous course as soon as they were left alone, as they did after circumventing stationary obstacles also. This was observed at all times of the day and not only in dense swarms but also with isolated individuals. It has been commented on by several authors (e.g. Faure 1894). Similarly, low-flying migrants, moving against the wind, did not become disorientated during complete lulls in the wind, but continued to fly in what had been an approximately up-wind orientation. This was also seen in isolated individuals, so cannot be attributed merely to gregarious inertia (p. 194). It is most readily attributable to the sun-compass-reaction, but this needs to be confirmed by further tests.

Landscape

Everyone who has seen migrating locusts is familiar with the way they, like other animals, avoid obstacles in their line of flight. Their neat dodging manoeuvres are most striking when the obstacle is moving, such as a man trying to catch them, but it is no less apparent when the obstacles are stationary, like trees, when a swarm (as observed on 15 June 1943 in the tamarisk grove already mentioned) breaks up into streams moving along open lanes between the trees, the streams diverted here and there by trees in the way, but keeping their general direction. It seems certain that the reaction is a visual one, for it occurs quickly and precisely and regardless of whether the obstacle is up-wind, across-wind or down-wind. Some crude trials of this reaction were conducted in Iran utilizing an artificial obstacle which did not in fact obstruct the path of the flying insects, but merely obtruded itself suddenly into their visual field. This was a 7 m. square of black cloth spread on the ground when low-flying migrants were passing. The original intention had been to see whether migrants could be induced to settle by a strikingly dark and conspicuous object in their path.

On the first occasion, near Kerman on 20 May 1943, the locusts were flying in sunshine over a great expanse of light fawn-coloured gravel with which the black cloth contrasted sharply. A thermometer showed the same reading at 1 m. over the black cloth and over the bare ground. The locusts were migrating steadily in loose groups or as isolated individuals. During 30 min. of observation none hesitated, swerved or settled anywhere in sight except near the cloth. Nor did any settle actually on the cloth or within 1 m. of its border. But, out of about fifty individuals that passed over the cloth at a height of 3 m. or less, a substan-

tial minority hesitated and turned away momentarily when over or near the cloth, resuming their previous course as they passed away. Four individuals suddenly changed course when over the cloth, came down and settled on the gravel within 3 m. of it. Twelve others did not change course, but came down and settled on the gravel within 15 m. of the cloth after passing over it. None of the hundreds that passed over the cloth above 3 m. descended, but about twelve flying at 5 to 10 m. came down and settled 3 to 5 m. *short* of the cloth. The fact that higher fliers responded before passing over the cloth but lower fliers afterwards, is contributory evidence that the response was visual, for the higher fliers would see the cloth sooner than lower fliers.

The cloth was spread again later on that day, but locusts were fewer and flying rather higher, while the background was less suitable. It was a light sandy patch in a dry river bed, but nearby and along the locusts' flight route there were many patches of contrastingly darker ground, and the sun was obscured. No responses to the cloth were noted.

The black cloth was spread a third time, together with a red one, on open, light-coloured ground on 13 June 1943. During 30 min. about five hundred locusts crossed each cloth within about 3 m. above it, and many more at greater heights. This time there was a certain amount of spontaneous settling, for nineteen low-fliers came down and settled elsewhere in the vicinity nowhere near a cloth. But no sudden changes of direction occurred elsewhere in the vicinity, whereas many fliers hesitated on passing over the cloth, veered away, resumed their original course and flew on. Perhaps fewer locusts were caused actually to settle by the cloth on these second and third occasions because the locusts had been flying already over a variety of backgrounds. In the first exposure of the cloth the locusts had had no such distraction for perhaps hours *en route*, and the black patch must have been a very novel feature in the landscape for them.

The results of these trials showed that migrants could not be caused to settle in appreciable numbers by a black conspicuous object. More interesting, however, was the fact that many did react to it as they passed over by hesitation and change of direction, soon corrected. Settling appeared to be merely an extreme form of the reaction to the same kind of stimulus.

The question naturally arises as to whether such effects occur also on a much larger scale when their importance would be correspondingly greater. Unfortunately, it is impossible to distinguish the visual effects of large-scale physical features from the other effects of such features, such as changes in wind, temperature, etc., but one or two field observations may be mentioned here.

Near Bandar Abbas, Iran, on 27 April 1943, a large, loose, pink swarm extending from the ground up to about 50 m. was 'rolling' in little wind across the level floor of a wide valley. In front of it was a steep-sided ridge 150 m. high. On coming up against this wall many fliers settled at its foot, but others turned and flew along it until they drew level with a gap where the ridge was only 50 m. high, whereupon they turned into their old direction and streamed through the gap.

Direction changes in face of a change in the visual field, but without any solid obstacle in the way, were observed among Desert Locust swarms reaching the coast of Algeria in June 1944 (personal communication from Mr G. F. Burnett). A swarm was observed traversing the coastal plain near Reghaia, about 25 km. east of Algiers, on 16 April 1944. The locusts flew north-north-east toward the sea, across a light westerly wind, and extended

from the ground up to about 100 m. On reaching the shore-line the leading locusts turned back into the main body. General confusion resulted, but out of it a new direction of flight emerged, now along the shore-line to the west-north-west. On the 21st a second, larger swarm appeared flying northwards. On reaching the shore-line the locusts again did not cross it but drifted along it, now in one direction and now in the other. In these cases there may, of course, have been a change in the condition of the air at the shore-line, and the locusts' change of direction was not necessarily due to the sight of that line. But here again, the comparable behaviour of marching hoppers (Kennedy 1945) when stimuli other than visual ones could more safely be ruled out lends some support to the view that the adults were reacting mainly visually.

The opposite of obstacle-avoidance, that is, *attraction* to conspicuous objects, was also observed, but not among migrants in full flight. For example, fledglings were observed for some days in June 1943, in and around the luxuriant oases (walled gardens) or tamarisk groves, both surrounded by arid wastes, in the district south of Bam on the edge of the Dasht-i-Lut (south-east Iran). Hoppers had developed all over the area. The fledgling adults did not migrate *en masse* for a week at least, but every day they flew in loose flights for short periods, frequently brought down by the wind and never progressing far. In the course of these flights they collected in large numbers in the oases. Once they reached an oasis they may have been held there by a number of features such as food, shelter from the wind and the noticeably lower temperature and higher humidity, but it was obvious from direct observations that they were also held by visual attraction to the conspicuous trees and buildings. When they took to the air they were often carried out on to the bare ground, but rapidly flew back to the oasis even if this meant unusual exertions for them in flying against the wind. Since the return to the oasis or tamarisk grove was also made across or even down-wind, it could not be attributed then at any rate to any wind-borne moisture or odour. The attraction was most evident toward evening when the locusts abandoned the open ground altogether and collected in the oases or on any trees, even isolated ones, outside it.

Again, clumps of trees, the most conspicuous feature of the immediate landscape, were pointed out to us by farmers in Kenya as the habitual roosting sites of any swarms that settled in the locality. The locusts either settled directly on these clumps as migration slackened toward evening, or they settled in the fields and later flew up into the trees before nightfall. Of settled swarms observed by us, all were crowded on the tallest vegetation available. If that consisted of only a few shrubs and small trees these were heavily laden with locusts, with the rest of the swarm less thick on the ground. One swarm was found settled at Morendat, Kenya, on 22 April 1944, in park-like country with irregularly spaced trees of various sizes, and the locusts had gathered almost exclusively on the upper parts of the tallest of them.

REVIEW AND ANALYSIS

Influences affecting swarm behaviour

The condition of the locusts

The fact that full migratory flying does not appear immediately after the final moult, but develops gradually, was made clear by Uvarov in his book (1928; see also Predtechensky 1935*b*; Khan 1945; Johnston & Buxton 1949). Further aspects of this process, brought out

here (pp. 173–175), are that the hardening of the cuticle is not complete even when the young locusts have started persistent mass flying, and that, associated with the softness of the body perceptible for a number of days after the last moult, there is a lack of power in flight, reflected in the inability of fledglings to make headway against weaker winds than fully hardened locusts. In this way fledglings develop the habit of persistent flight before they are strong enough to resist carriage by the wind as well as older migrants do, which is likely to make a considerable difference to the large-scale, *resultant* effects of their migratory activity (Part II).

The reduction of migratory activity around the time of mating and egg-laying, observed during the present studies, was also indicated by Uvarov (1928), who wrote that a period of ‘daily circular flights without any definite direction’ preceded oviposition. The reduction in migration is not apparently due to direct preoccupation of the insects with reproductive activity, for in any swarm seen mating and laying there are many individuals not participating in these activities but yet not migrating. In addition to the direct loss of flying time through engaging instead on mating, laying and associated activities, there seems to be a reduction in the effort put into such flying as is done (pp. 175 and 192). In this respect sexually active locusts come to resemble fledgling locusts, in their resultant behaviour with respect to wind, so that locusts in these two conditions have been classed together as *semi-migrants* (p. 173). But the reduced migratory activity of sexually active locusts is not due to physical weakness, as in fledglings (pp. 173–177), and must be attributed to some transient physiological inhibition. Whatever the internal cause may be, it has the effect of permitting reproductive activity to develop fully without interference from the locomotory activity which preoccupies the insects so strikingly all the rest of their lives.

It has been suggested that sexual maturation affects migration not only incidentally, in the way just mentioned, but quite fundamentally, being its real cause. Uvarov (1928, p. 86) wrote:

‘...physiological factors, which must be considered the real cause of flight. There can be no doubt that the emigration flight is intimately connected with the process of development of the genital products. An internal stimulus for the flight during the maturation of genital products is prevalent in other insects, such as termites and ants, in which a so-called nuptial flight precedes copulation; this is exactly what happens in locusts.’

This idea has found no place in Uvarov’s subsequent writings, but deserves mention because it has been widely accepted, for instance by Imms (1937, p. 306), although it will not bear examination in the light of the facts.

In undertaking migration, adults are merely resuming an activity which is no less characteristic of the same insects as hoppers. Adults employ a more spectacular form of locomotion, flight, when migrating, than do the hoppers which can only walk or hop. But the behaviour of adult gregarious locusts is recognizable as migratory because of the extraordinary *persistence* of their locomotion, not because of its particular form. The locomotory activity of hoppers is no less persistent, being interrupted only by moulting, given favourable conditions. Adults resume migration while they are yet fledglings and continue to migrate, with interruptions, when their sexual organs and behaviour are fully developed, even until they die (p. 175 and Waloff 1946*a*, p. 63). In the normal course of events

gregarious Desert Locusts grow, live and die as migrants. Migration is thus a fundamental property of the insects, not connected with any particular stage of their physiological development.

Wind

General. Wind is probably the most frequently cited of all possible influences upon adult locust migration, and yet is the one over which there is least agreement.

It will be seen in later sections that the behaviour of migrant adults resembles that of hoppers in many ways. Since hoppers, being earth-bound, are easier to study, it is often possible to use hopper observations as pointers for the analysis of adult behaviour. That is done in this paper, for the ultimate aim here is to distinguish what is essential from what is derivative in the behaviour of migrants, whether they be hoppers or adults. If adult migration has usually been considered by itself, apart from hopper migration, it is the role of the wind in adult behaviour which must be held mainly responsible, for it has seemed as puzzling as it was obviously important. Adults fly: they leave the hoppers' fixed substrate, the earth, and move in a medium, the air, which itself moves in a complicated manner. This could hardly fail to impose a new resultant pattern on their behaviour even if in essentials it were the same as that of hoppers. Hence, as a necessary step toward distinguishing those essentials, attention was concentrated on the role of the wind in the present studies on adults.

The evidence we have concerns the effects of wind on the speed, height, frequency and direction of flight.

Some impressionistic evidence is available that low fliers regulate their air speed according to the wind speed (p. 177). If this were confirmed, estimates of the air speed of low-flying locusts would vary with the wind speed. No general validity could then be attached to the figure of 15 ft./sec. (4.6 m./sec.) recorded by Mr J. F. Graham in Kenya in 1946, although this was quoted by Gunn *et al.* (1948, p. 45) as the 'first measurement of air speed made by a rigorous method'. Mr Graham kept pace with a locust while carrying an anemometer and so obtained the true value of that locust's air speed at that moment. But the very rigour of his method, excluding as it did the wind speed from measurement and therefore from attention, restricts the value of his result.*

The following estimates have been published of the flying speed of Desert Locusts explicitly stated to be in calm air near the ground: 3.1 m./sec. (Hall 1840); 4.2 m./sec. (de Lépiney 1928); 2.7 m./sec. (Cheesman 1929); 2.7 m./sec. (Williams 1933); and 8.0 m./sec. (Rungs 1945). Apart from Rungs's exceptionally high figure, these estimates of locust air speeds, under conditions when these were also ground speeds, are rather strikingly alike. Observers in Algeria (1929) gave similar figures, 2.8 to 4.2 m./sec., for the 'normal' speeds (presumably *ground* speeds) of swarms under unspecified wind conditions and at unstated heights; while a similar range of *air* speeds, 2.5 to 4 m./sec., is given here (p. 177) for locusts flying low against light winds. Mr Graham's figure of 4.6 m./sec. in unknown wind approaches the mean figure of 4.9 m./sec. in a variety of conditions given by Rainey & Waloff (1948). Perhaps these higher figures were due to the locusts increasing their air speed against head-winds, and an observation of Gunn *et al.* (1948, p. 45) is noteworthy in this connexion. A swarm was observed flying low, at a ground speed of about

* Also, the speed of Mr Graham's locust may have been influenced by his very pursuit of it.

1.8 m./sec., although opposed by a wind of about 4.6 m./sec. It must therefore have been maintaining an air speed of more than 6 m./sec. Waloff & Rainey (1951) found that the calculated, instantaneous air speeds of a number of Desert Locusts flying at 3 to 12 m. above the ground (see p. 205), varied little, despite wide variations of wind speed. This leaves the question open, for it was only locusts flying closer to the ground which gave the impression, to the writer, of adjusting their air speed in relation to short-term changes of wind speed (p. 177). Further observations are needed both in the field and in the laboratory to see how far locusts do in fact regulate their ground speed in the way suggested.

The inverse relation between wind strength on the one hand and the height and frequency of flight on the other (p. 178) has often been referred to in the literature: by Koeppen (1870: *Locusta*), Künckel d'Herculais (quoted by de Lépiney, 1928, 1933: *Schistocerca*), Regnier (1931: *Schistocerca*), Zimin (1934: *Calliptamus*) and Zolotarevsky (1929: *Locusta*), and the present observations provide some quantitative evidence on the point.

It is over the relation between flight *directions* and the wind that there has been the most confusion in the literature. Among those who have made direct observations on a number of swarms in full flight, Ballard, Mistikawi & Zoheiry (1932: *Schistocerca*), Lean (1936: *Locusta*) and Gunn *et al.* (1948: *Schistocerca*) have described a preference for down-wind flight. Synoptic studies, that is, the mapping and analysis of all available locust reports in relation to the meteorological records, such as Lean's (1931*a*) analysis of the great outbreak of *Locusta migratoria migratorioides* during 1928–31, Waloff's (1946*a*) analysis of the movements of *Schistocerca* in East Africa, and Rainey & Waloff's (1948) study of Desert Locust swarm movements and air-mass trajectories over the Gulf of Aden, have shown general agreement between migration direction and wind direction (with-wind migration). On the other hand, Lean's (1931*b*) more detailed studies in Nigeria did not show such consistency, major movements being sometimes obliquely up-wind, sometimes directly up-wind and sometime down-wind, and he believed humidity was the key factor. In his review of the annual cycle of solitary and gregarious *Schistocerca* in India, Rao (1942) points out that the two major migration trends, that eastwards from the spring breeding areas and that westwards from the monsoon breeding areas, appear to be due to winds in those directions.

Many authors have contented themselves with stating general conclusions or impressions or describing isolated cases, and by these down-wind flight is again most frequently stressed (e.g. Lallemand 1865; Vosseler 1905; Andrews 1915; Vrydagh 1932; Bruzzone 1936).

There are a number of accounts of swarms flying with the wind in front of storms. For example, the following appears in an unpublished note by C. L. Collenette:

'On 23rd September, 1929, a large swarm passed over Buran (British Somaliland), flying south, exactly before the wind, which was moderately strong. The main body was perhaps 500 ft. up, and made much noise. From the direction from which they came, rain clouds and rain could be seen, but this did not reach Buran.'

In the same country and year, Farquharson (1930) described a succession of enormous swarms migrating southwards at great height immediately in advance of heavy rain. A reliable observer, living near Eldama Ravine with a commanding view over the Kamasia Reserve toward Lake Baringo, Kenya, informed me he had often watched swarms flying southwards against the prevailing wind, in 1944 and previous years. Time and again, he

reported, a swarm would fly slowly but steadily on up the slopes in the sun until met by a rainstorm blowing up from the south. Thereupon the swarm was thrown into confusion for a few minutes and a new, reversed direction of flight emerged, the swarm now flying fast with the wind back to the sunny lowlands, whence it returned later, flying slowly up-wind again.

Even among authors giving only general conclusions or quoting isolated cases there are several who stress up-wind flight (v. Frauenfeld 1870; Faure 1894; Siyazov 1928; Cheesman 1929; Zolotarevsky 1929; Allan 1933; Predtechensky 1935*a*). It is among the longer-range movements that down-wind movement is most apparent, but at least one major migration trend by *Schistocerca* is against the prevailing wind: the northward movement in spring in North Africa, Arabia, Iran and Baluchistan. Waloff (1946*a*, p. 50) found evidence of a tendency for old mature swarms to move against the prevailing wind in East Africa even when younger swarms were not doing so. Key (1942) found a definite up-prevailing-wind preponderance among numerous records of *Chortoicetes terminifera* swarms.

Finally, every field observer has seen swarms flying neither against nor with the wind, but across it, or in so little wind as to make it virtually inconceivable that it was exerting any directing influence, while yet the locusts showed at least as much unanimity and stability of orientation as they do when flying against or with the wind.

In seeking to bring some order into this confused field, authors have adopted very different approaches. Fraenkel (1932), reviewing the subject of insect migration at a time when much less information was available on locusts than to-day, concluded that they were often carried on the wind but did not actively orient to it. To-day, however, our fuller information on locusts presents a superficially confused picture similar to that Fraenkel then described for butterflies. Yet, while recognizing the lack of any fixed relation between migrant butterfly directions and wind directions, Fraenkel insisted that this did not exclude the possibility of causal role for the wind in many of the cases when with- or against-wind migration was reported, and he discussed means by which flying insects might orient actively on the wind (see below).

Waloff (1946*b*) and Rainey & Waloff (1948), on the other hand, chose for analysis some rapid, long-distance swarm movements made when 'the wind speed is greater than the air speed of the locusts' so that the 'down-wind displacement would in fact occur even in the complete absence of any persistent orientation', and when the locusts were crossing the sea and so presumed to be obliged to remain air-borne. This approach undoubtedly simplifies the situation, thereby enabling the meteorological aspects of a certain type of resultant displacement to be worked out, but it should not lead us away from the biological aspects of migration.

Williams (1930, 1942, 1949) and de Lépiney (1928, 1933) do not merely leave on one side the orienting influence of the wind; they make out a case against it, except at the moment of taking off. They draw particular attention to cases where the locusts' courses seem to be entirely independent of the wind. De Lépiney stresses that the wind participates as a vector in determining the tracks of migrants, but believes their courses are independent of the wind. Williams minimizes the wind's role not only as an orientator, but also as a transporter of the migrants. Recognizing that a correlation between flight directions and prevailing wind directions often exists, he attributes it to chance, or to a 'psychological error' on the part of observers who unconsciously record flight directions as more accurately against or with the

wind than they in fact are, or tend to classify them into only two categories, against or with the wind. This tendency cannot be denied, and it means that the accumulated records of butterfly directions, for example, which show a clear preponderance of flights against or with the wind, are nevertheless unreliable evidence of any real preference for flight in those directions. But if such records are valueless for the purpose of revealing a real preference strong enough to emerge from a mass of records taken under all sorts of conditions, they are equally valueless for the purpose of revealing something more probable: a preference exercised in certain circumstances, but not in others. Such records prove neither the presence nor the absence of active wind orientation.

Both Williams and de Lépiney take the view that, since the direction of migration does not show a constant relation to the wind direction, some other environmental feature must be the real key to the orientation of migrants, and that therefore the wind's possible orienting influence can be disregarded. As against that view, Kennedy (1948) and Gunn (1948*b*) have argued that the wind is one of many influences each of which is capable of determining orientation in some circumstances, but not in others; hence we need not seek some *one* environmental key to the orientation of migrants. Gunn *et al.* (1948), accepting the possibility that courses as well as tracks may be influenced by the wind, advanced the hypothesis of the 'forbidden course' (discussed below, p. 222). However, the main conclusion they drew from their observations was that the diversity of flight direction—wind direction relations excluded at any rate 'some of the simplest hypotheses' concerning the wind's directing influence, such as that locusts always fly up-wind, or always down-wind. Since it was that same conclusion which led Williams and de Lépiney to disregard wind altogether as an orienting influence, it cannot be too strongly emphasized that the diversity of flight-wind relations is entirely to be expected, considering that locusts fly in winds ranging in speed from well above to well below their own air speed. Hence, so far from providing grounds for disregarding the wind's possible orienting influence, the diverse flight-wind relations demand closer analysis, before any conclusions can be drawn concerning that influence. This point was made originally by Fraenkel (1932) when he wrote his review of insect migration.

In embarking on the analysis we must revert, therefore, to the simple and fundamental, but neglected, point made by Uvarov (1928, p. 86) that 'when there is no wind, or only a slight breeze, the flight is not affected, though strong winds always carry the swarms with them.' 'Always' is rather too strong a word, since the locusts often settle rather than let themselves be carried, but the fact remains that in strong winds, which exceed their own air speed, locusts must go with the wind if they fly at all. Certain authors (d'Herculais quoted by de Lépiney 1928; Egypt 1916; Regnier 1926; Zolotarevsky 1929) have long gone further than this, noting the tendency of low-flying locusts to fly up-wind in light or moderate winds and to an increasing extent down-wind as the wind speed rises. It has also been known for a long time that the orientation of flying locusts can vary according to their height above the ground, for Williams (1933), Predtechensky (1935*b*) and others have recorded instances like those cited here of swarms consisting of a lower layer of up-wind fliers and an upper layer of down-wind fliers.

Such observations pointed the way for further work which would eventually lay bare the causal connexions between the wind and migratory behaviour. But these pointers have not,

in general, been followed up. The data so far available have been collected without sufficient regard to the various circumstances which could have been expected, in the light of existing observations, to make important differences to the locusts' behaviour. As a result, the collected data present a confusing picture and the only kind of generalization possible is a negative one, such as that of Gunn *et al.* 1948 (mentioned above, p. 204) or the following:

'If in any district there is a prevailing wind, and also a more or less regular direction of migration, an apparent relation between wind direction and flight is bound to appear although it will be no evidence of cause and effect' (Williams 1942, p. 233).

Williams went on to quote his observations on locusts which showed a preponderance of flights more or less against the wind. 'But', he continued, 'as neither all possible flight directions nor all possible wind directions occurred one cannot draw any conclusion.' This statistical approach, which seeks mainly to increase the *quantitative* bulk of data, tends to lose sight of the qualitative diversity of such biological events, and to defeat its own end by postponing the drawing of conclusions until all possible flight directions and all possible wind directions shall have been recorded.

The bewilderingly confused picture presented by the data published hitherto on flight direction in relation to the wind seems to be due, in other words, to the tendency to look for some fixed relation, unaffected by varying circumstances. 'Ambiguous' observations, for example, of flight both up-wind and down-wind at the same time (above), have therefore been regarded as evidence against the wind having any important directing influence. That in turn has meant inattention to the wind's speed, to the height of flight, to the courses as distinct from the tracks of fliers, to the condition of the locusts, and so on.

A more systematic study of locust flight direction in relation to wind is that of Gunn *et al.* (1948, p. 45), who recorded all the above quantities except height of flight. They observed predominantly down-wind tracks at all wind speeds down to about 1.2 m./sec., and against-wind orientations only at still lower wind speeds. This appears to contradict my own findings of predominantly up-wind flight in winds up to nearly 4 m./sec., but their data refer solely to swarms that were just launching on migration in the morning and may not have attained their full, cruising air speed. Gunn *et al.* observations on swarms in full flight are fewer and are not accompanied by the circumstantial data necessary for comparative purposes.

The most detailed contribution to this subject is by Waloff & Rainey (1951), who emphasize that behavioural preferences cannot be deduced from a series of observations on separate swarms. A mobile observer can make contact with swarms flying slowly up-wind, more frequently than with swarms flying faster down-wind (cp. part II, footnote on p. 275), and the bias so introduced must not be mistaken for a preference of the insects. It was for this reason that more importance was attached in the present account (pp. 182-193) to variations of behaviour during continuous observations on single swarms, than to the collected records from all swarms. The latter are regarded only as confirmatory, and that only after they have been classified according to criteria suggested by the continuous observations.

Waloff & Rainey recorded the instantaneous courses and tracks of individual fliers, using a mirror 'flight direction-finder' (figure 7), with simultaneous readings of wind speed and direction, in the course of four periods spread over $4\frac{1}{2}$ hr. observation on a single

Desert Locust swarm. The *mean* course of the locusts remained between 8 and 24° to the left of due up-wind during the first three periods, thereby following the progressive shift through about 40° which the wind underwent in that time. A number of the individual courses were within 15° of due up-wind in all four periods, so long as the wind speed did not exceed about 3 m./sec. But none were so close to due up-wind in stronger winds; and in the fourth period, when the wind was more gusty (exceeding 4.5 m./sec. twice as often as it had before), the mean course deviated from the mean wind direction by 57° . These findings are in general agreement with the present account, with the important addition of the evidence of locust courses changing with slow changes of wind direction. Waloff & Rainey analyzed their individual records further, to see whether the effect of gusts was to cause the locusts to turn out of their up-wind orientation to the extent necessary to avoid backward drift, as suggested on p. 184. They found no evidence of this, but 'snapshot' readings are not suitable for demonstrating the existence or non-existence of such a reaction, as emphasized on p. 186. They take no account of the previous wind or previous behaviour of the locusts, in a situation where both are varying rapidly, both from moment to moment and between locust and locust. A very large number of readings would be required to build up a connected picture of the fast-moving manoeuvres of any one individual in such winds. Moreover, Waloff & Rainey's readings include locusts flying at all heights from 3 to 12 m. That is a critical range of heights, to judge from the observations recorded in the present paper, so that aggregating the readings for analysis may have concealed some regularities.

My own and others' observations which are quoted earlier (pp. 182–193) were not made systematically or with the desirable degree of precision. But attention, at least, was paid to all the circumstantial points mentioned above. Considered together, the observations provide certain indications of an orderly system of flight direction–wind direction relations dependent on wind speed and height of flight. These results, together with the findings on the effect of wind speed on flight activity and on the height of flight, make it worth while to consider how the wind may in fact affect the behaviour of the locusts, first as a direct mechanical stimulus to them and secondly as an indirect cause of visual stimulation.

Reactions to direct stimulation by wind. It is sometimes assumed (e.g. by Zolotarevsky 1929) that flying insects can sense the direction of the wind directly, by its pressure on their bodies, even if the wind be completely smooth. This seems to be a misunderstanding, as Fraenkel (1932), de Lépiney (1933), Kennedy (1940) and Williams (1942) have pointed out. Any object which exactly floats in air and which does not exert any propelling force tends to acquire quickly the velocity of the air. In a completely smooth wind, once the velocity of the wind has been reached, such an object cannot have any wind force acting on it. If the object is self-propelled then the only wind force acting upon it will be that due to its self-propulsion through the air. Thus a locust flying in a smooth wind cannot receive any direct information about the wind speed or direction and cannot therefore react directly to it.

If, on the other hand, the wind is not smooth but gusty, then at each gust an additional force, not due to its own propulsion, will act on the locust. Williams (1942) discussing the problem of wind as a directing influence for migrant insects, has drawn attention to the work of Giblett (1932) on the structure of the wind. Under adiabatic or superadiabatic air conditions, common during the day in clear weather, Giblett concluded (p. 56):

‘...there are major eddies composed of alternating masses of fast and slow moving air, while embedded in the air masses there is a large number of small scale eddies. These air masses are considerably longer in the direction of the wind than they are broad. The changes of velocity in wind from air mass to air mass are characterised by abrupt increases and comparatively gradual decreases... These facts have been found in eddies which are on the scale of 4000 ft. long by 600 ft. wide (these measurements are probably below the average). There is another group of major eddies which ranges up to a dimension in the direction of the wind of the order of 10–20 miles.’

The major eddies, according to Giblett, show the same abrupt rise and slow fall in wind velocity, while the numerous, small-scale eddies are not elongated in the wind direction.

The elongation of the air masses in the direction of the wind might provide an observer, who was himself being borne by the wind, with a clue as to its general direction. As Williams (1942) says: ‘An insect would be subjected to a pressure from the direction from which the wind is blowing during the sudden advent of a gust, and a much weaker pressure on the opposite side as the gust dies away.’

In order to respond to these forces, the insect would have to be equipped with suitable receptors which would record the fact that some part of its body was taking up the new wind speed more quickly than other parts. The wings themselves could act in this way: locusts observed being carried on a gusty gale sometimes had their wings blown forwards over their heads (p. 183), the flat wings being more readily caught by the wind than the body (cp. Williams 1930, p. 384). But there was no evidence that these locusts were orienting to this unusual situation, for their orientation was the same as that of locusts flying in winds that were strong, but not violent enough to blow their wings forward over their heads.

There is, however, evidence of the existence of special aerodynamic sense organs on Acridids, in the shape of patches of hairs on the frons and vertex which are sensitive to the flow of air past the head (Boyd & Ewer 1949; Weis-Fogh 1949). Stimulation of these has been shown to initiate flight itself once the insect is deprived of a foothold and, during flight, to initiate contra-lateral (compensatory) turning responses when the air flow comes from one side instead of dead ahead. These responses could clearly have a stabilizing effect on the locust's flight direction, correcting its own deviations from a straight course, like the halteres of flies (Pringle 1948). Since the same receptors would presumably record a change in the wind direction, if that were sufficiently sudden, the responses could, conceivably, serve to orient the flying locust on the wind, but this is more conjectural.

At present, there is no observational evidence that locusts do orient themselves to the wind by such direct responses. The fact that the observed responses to wind changes were less marked away from the ground, where the wind is stronger, than they were close to it (p. 209), argues against direct responses to air movement participating in course and track determination, however important they may be in securing stability in flight. Moreover, if it is only the large-scale air eddies which are so shaped as to give the locusts pushes which are biased in the wind direction, while between these the insects are subjected to more numerous, randomly directed pushes, then it becomes very difficult to conceive how the insect could utilize its aerodynamic sense organs for orientation to the wind. It is also difficult to see, at present, how the same organs could be used, without confusion, for regu-

lating two quite different kinds of changes in the insect's relations to the air: both the changes due to its *own* aberrations, of pitching, rolling and yawing (that is, for flight stabilization); and, at the same time, the changes due to aberrations in the *air's* movement, independent of what the insect is doing, such as gusts (that is, for wind orientation, etc.). On the other hand, it would seem an economical employment of the means at its disposal if the insect used its aerodynamic sense organs, which are essentially directional *accelerometers*, for flight stabilization, and used other sense organs, such as the eyes, which can act as directional *speedometers*, for wind responses.

It remains to consider the effects of the wind as a direct stimulus acting on *settled* locusts. When the locust is resting on the ground it has a fixed standard of reference and is therefore in a position to sense and respond to the direct mechanical pressure of the air even when the wind is quite smooth. This may well account for the fact that locusts taking off in any appreciable wind are nearly always observed to be oriented into it.

It was observed that a sudden lull after a period of strong wind led to mass taking-off by settled locusts (pp. 178–181). Since locusts have a powerful tendency to fly spontaneously, the mass taking-off observed as soon as the suppressing influence of strong wind is removed doubtless represents the release of their spontaneous flight activity. A drop in wind was followed by mass taking-off over a considerable range of wind speeds, so that the decrease in wind itself rather than a decrease to a certain threshold wind speed was apparently what led to taking-off. It seems likely, therefore, that the 'damming-up' of spontaneous flying by wind leads to a situation in which a slight lull, to a wind speed which would previously have been quite effective in suppressing flight, releases flying with unusual unanimity. This may be the real significance of Zimin's (1934) observation that gusty winds were particularly effective in causing settled *Calliptamus* to take off. Similar observations have been made by Davies (1936) on aphids and Kennedy (1940) on mosquitoes.

It is noteworthy, however, that among a number of locusts caused to settle by a gust, those remaining in more exposed, insecure situations took off again sooner than those secure in better shelter (p. 181). Locusts settled in a strong wind are visibly affected by it. They can be seen bracing themselves against the buffeting, their antennae raised and quivering in the wind. Their immediate response is not to fly but to cling tenaciously to their foothold. But perhaps this stimulation adds to the strength of the pent-up tendency of the insects to fly, leading to mass taking-off whenever the wind's immediately inhibiting influence is relaxed in a lull. Further data are required to decide whether taking-off would occur in this way, as a relief from excessive buffeting.

The optomotor theory of behaviour in wind. While there is no evidence that flying locusts do, in fact, respond directly to the wind, there is good evidence that other insects make visual compensatory responses to the apparent movement of the fixed background, a movement due to their being carried over that background by the wind. The use of fixed visible features for wind orientation has been suggested for many insects, and demonstrated in the laboratory for mosquitoes (Kennedy 1940). It would, on the whole, be more surprising if locusts did not respond indirectly to wind in a similar way than if they did. What positive evidence is there that they do so react?

Perhaps the best evidence comes from observations of flight over water (pp. 192–193). When locusts were flying low against the wind over tree-dotted farmland, and the wind

increased to more than their air speed, they either reoriented down-wind, or flew lower, or even settled; they never underwent a sustained backward drift. But locusts flying over water did not appear to react to the wind in any of these ways and were, therefore, drifted backwards. The locusts over water did not react to the wind either directly or indirectly, while those over the land did. Beall (1941, 1942) made somewhat similar observations on Monarch butterflies (*Danaus plexippus* L.). Such behaviour is consistent with the idea that active responses to the wind require a visible background, the features of which, when prominent as on coarse-patterned land, may induce responses up to a fair height, but when small and inconspicuous, as on reasonably calm water, induce responses only at a much lower level.

Comparable, but less clear-cut indications that reactions to wind were in fact reactions to the apparent movement of the background pattern, came from the observations over land. Locusts flying well above the ground appeared to be less consistently oriented into wind and less responsive to changes in wind speed than those seen flying close to the ground at the same time (pp. 177, 179 and 183–185). This is the opposite of what we should expect if the wind acted mainly as a mechanical stimulus, for its speed increases with height. But it is just what we should expect if the wind acted mainly indirectly, through visual responses. Both the apparent size of the elements in the background pattern, and their apparent speed of movement, decrease with increasing height above the ground, so that the movement of a given background pattern would often be inappreciable to higher fliers while remaining noticeable enough to evoke responses from lower fliers.

The field observations thus suggest that the behaviour of locusts in wind depends on optical responses to the apparent movement of the ground, such as have been demonstrated in the laboratory for mosquitoes (Kennedy 1940). But the field data on locusts are made up to a great extent of impressions; hardly adequate material, by itself, for proving the optomotor basis of locust behaviour in wind. Let us, therefore, first recapitulate the experimental results with mosquitoes and the theory deduced from them, and then see if the locust data are consistent with this theory.

The mosquitoes, *Aedes aegypti* L., were tested in a small wind tunnel over a striped floor. They showed a strong preference for flying against the wind. They maintained a ground speed of about 17 cm./sec., both in still air and also against winds up to 33 cm./sec., so that in the latter case their air speed was about 50 cm./sec. When the wind speed reached 100 cm./sec., their air speed could usually be increased no further and the mosquitoes were flying without making any headway. But, rather than turn or allow themselves to be carried backwards, they then alighted on the floor. With the air and the floor stripes still, the mosquitoes flew in all directions. If the floor stripes were then moved, the air remaining still, mosquitoes flying against the direction of stripe movement reduced their air speed, wavered and then turned right round to fly with the stripes. By the time the stripe speed reached 13 to 17 cm./sec. all the mosquitoes were flying in the same direction as the stripes. They often flew faster but never more slowly than the stripes, increasing their air speed as the stripe speed increased.

Now the wind, carrying an insect, creates for it an apparent movement of the background which is in the direction opposite to the wind's own direction, so that a preference for flying against the wind is the visual equivalent of a preference for flight with moving stripes. Thus

the mosquitoes' behaviour in moving air over still stripes, and over moving stripes in still air, evidently both depend on visual responses to the movement of the stripes relative to the mosquito, and experiments in darkness provided direct proof of this. The movement of a stripe relative to the mosquito can stimulate it only as an image passing over the retina, and a given retinal velocity can be produced by the mosquito's flight alone, by its being carried by the wind as well and, in experiments, by movement of the striped floor.

These facts indicate that the mosquito has a *preferred retinal velocity*, divergences from which evoke compensatory responses. Three types of response were observed:

- (1) change of air speed,
- (2) change of orientation,
- (3) settling.

In the original account of this work it was suggested that compensatory responses were evoked whenever the retinal velocity departed from some supposedly 'normal' range: that experienced in free flight in still air over a still background. This suggestion took no account of the fact that the retinal velocity experienced under such conditions would vary with the insect's height above the fixed background, for this point was not examined in the experiments in the small wind tunnel. The more familiar concept of a *preferred* retinal velocity is introduced here in place of the indeterminate 'normal' velocity. By the preferred velocity is meant simply that which the insect's various responses tend to restore, and it is apparent that *what is preferred is the movement of images directly from front to back over the eye, at a certain moderate rate.*

Thus the various responses are not compensatory in the absolute sense of serving to nullify all movement of images in the eye; that would render locomotion impossible in the presence of visible fixed objects. Nor are the three types of response independent of one another. They are all evoked only by deviations from a tolerated or preferred retinal velocity and form an integrated system, one kind of response being replaced by another when the first fails to restore the preferred retinal velocity. For example, when the speed of movement of images from front to back over the eye is reduced by a head-wind, the insect compensates by increasing its forward air speed. When the speed of image movement from front to back is reduced to *nil* and movement begins in the opposite direction, owing to a head-wind so strong that the insect cannot compensate by further increasing its air speed, the insect counteracts the tendency to backward drift in another way, by settling. When the speed of image movement from front to back is increased, by the movement of floor stripes against the direction of the insect's flight, it compensates by reducing its air speed. When this fails to restore the preferred retinal velocity because the stripe speed is too high, the insect compensates in another way, by turning round and flying in the same direction as the stripes, thereby reducing the front-to-back retinal velocity. When the same situation of excessively fast front-to-back image movement is created by a tail-wind, the insect turns round, into wind, with the same result.

Similarly, it was suggested that when the images pass transversely, say from the left to right instead of directly from front to back over the eye, owing to a cross-wind from the right, the insect compensates by following the direction of the transverse image movement, that is, by turning toward the right until it is facing into the wind and transverse image movement has therefore ceased. That kind of compensatory response was held responsible for the insects'

strong preference for flying against the wind rather than in any other direction. It is now suggested, further, that this kind of reaction, determined mainly by the *direction* of image movement over the eyes, may be what prevents the insect from abandoning its up-wind orientation even when the *speed* of the image movement has fallen well below the preferred value and could be raised by turning down-wind.

Although less precise, the field observations on locusts are at least consistent with the experimental observations on mosquitoes. The locust evidence is weakest concerning the regulation of air speed according to wind speed (pp. 201–202). This type of reaction was recorded only as an impression, and only in observations on low flights against the wind. Reduction of air speed when flying down-wind, which would be equivalent to the mosquitoes' reduction of air speed when flying against moving stripes, could not be detected among locusts in the field, if only because they passed too quickly from view. Reduction of air speed by mosquitoes flying down-wind in the wind tunnel could not be detected either, for a similar reason; the insects were quickly deposited on the end wall of the tunnel.

The locust evidence is better in the matter of orientation (pp. 182–193), with an apparent preference for up-wind courses, and a definite refusal to be carried backwards, when flying near the ground. This preference seemed to become more marked as the wind speed increased up to the point where settling began, as among the mosquitoes.

The third type of response noted among the experimental mosquitoes, settling when forward ground speed is drastically reduced by a strong head-wind, was clearly evident among low-flying locusts. The field observations emphasized an aspect of this behaviour which was detectable but not remarked upon in the small wind tunnel, viz. that settling is merely the end-point of a change-of-altitude response to excessive wind (pp. 178–182).

So far, therefore, the field observations on locusts parallel the experimental observations on mosquitoes sufficiently closely to warrant a strong presumption that locust behaviour in wind is also governed by optomotor reactions. The optomotor theory thus proposed for both mosquito and locust behaviour may be summarized as follows: *any image movement over the ventral ommatidia which diverges from the preferred velocity (rate and direction) evokes compensatory responses.*

There were some new features in the field behaviour of the locusts, such as changes of behaviour with height and the emergence of a preference for down-wind courses among higher fliers in strong winds. Such effects could not have been expected in the wind-tunnel experiments, for the mosquitoes were there forced to remain close to the 'ground' and had little room to manoeuvre in the horizontal plane also. But here again it seems unwise to use the largely impressionistic locust observations directly for an extension of the optomotor theory to free-air conditions. Instead, it is proposed to start from the firmer basis of the mosquito findings, with which the locust observations do not conflict, and work out hypothetically what would be the consequences of the optomotor theory under free-air conditions. Given the pattern of behaviour to be expected with various combinations of wind speed and height of flight, we can then re-examine the locust observations and see how far they conform to it.

The optomotor hypothesis of field behaviour in relation to wind speed and height. In elaborating this hypothesis we postulate not only the three types of compensatory response and the preferred retinal velocity, but also a *preferred air speed*, departures from which provoke

compensatory responses of the same three kinds. There is good evidence that gregarious locusts are very persistent fliers, which immediately sets a lower limit of preferred flight exertion, at somewhere above zero air speed. The long continuance of locust flying makes it seem likely, on general grounds, that there is also an upper limit beyond which they exert themselves only under pressure, preferring a moderate, 'cruising' air speed. At present there is no quantitative evidence of such a preferred air speed, however, and in any case it presumably alters with the condition of the locust. But if there were only a preferred retinal velocity and no preferred air speed, then one might expect swarms would quickly shear apart from the top down, the higher fliers racing ahead (during up-wind flight) to compensate for the lower retinal velocity due to their greater height, since retinal velocity decreases with height faster than the wind speed increases with height.

For simplicity of exposition, only courses directly up- or down-wind will be considered here. The detailed process of turning from one course to another and the not uncommonly observed maintenance of cross-wind courses are not considered, because the available data are inadequate and the hypothetical analysis would require further and more complicating assumptions.

The height-wind speed hypothesis is best explained by means of diagrams. These must be very schematic and are constructed for the present without any numerical scales or assumed values for the preferred retinal velocity and air speed. The co-ordinates in all the diagrams are height above the ground and wind speed, the latter being assumed for the present not to vary with height. The logical consequences of the various assumptions made are shown, by cumulative stages, in figure 13.

The most obvious consequence of the optomotor theory is that locusts flying sufficiently high will not show any compensatory responses to the wind, simply because they receive no optomotor stimulation. We may then describe them as above the *maximum compensatory height*.

The postulated 'preference' for a particular retinal velocity did not refer of course to a subjective preference for some ideal situation. The term preference is merely a convenient way of expressing the net result of the insects' reactions to changes in their retinal velocity. The postulated preference assumes *some* movement of images of background objects, with immediate changes in that movement whenever the wind speed or direction changes, or when the insect changes its air speed, direction or height. In the complete absence of such image movement, and when therefore nothing the wind or the insect does produces any immediate change in its retina, we assume it does not 'react': that is, no behaviour changes result from this situation in itself.

The maximum compensatory height can be set in two ways. With a given 'grain' size in the background pattern, there will be a definite height, independent of the wind speed, above which the locusts' eyes fail to resolve the separate elements in the pattern (figure 13*A*, *JJ*). Below that height they will be able to resolve the pattern and so be able to be stimulated by its apparent movement, provided that movement be at an appropriate rate.

Even if the background pattern can be resolved up to infinite height, the movement of images of the insect's eye will sometimes be too slow to evoke any responses. It will be fast enough to evoke them only if the insect's ground speed is above a certain value, which will

over the eyes of a rising locust will become too slow to evoke compensatory responses will depend on the speed of the wind carrying the locust, as well as on its own air speed and course, for its ground speed depends on all three. The stronger the wind, the higher the

locust can rise before its apparent ground speed (retinal velocity) will fall below the stimulatory threshold (figure 13*B*, *KK*).

These two kinds of limitation, illustrated in figures 13*A* and *B*, are combined in figure 13*C*. With the field observations in mind it is assumed that, over the range of wind speeds with which we are dealing, the limiting factor is usually the locust's inadequate ground speed. Only when the wind speed is very high, along *LJ* in figure 13*C*, do we assume that non-resolution of the background pattern sets the height limit for optomotor responses. Thus the first consequence of the optomotor theory is that there will be a *maximum compensatory height* along *KLJ* in figure 13*C*, which increases with the wind speed as long as the locust's eyes are capable of resolving the background pattern. Correspondingly, there will be a *minimum compensatory wind speed*, also along *KLJ*, which increases with height.

Above the maximum compensatory height the locusts' movements will be affected only mechanically by the wind. Their courses will not be affected by the immediate wind, unless they can orient by reactions to mechanical pressure changes (see pp. 206–208). The courses of the insects will not necessarily, of course, become random in this situation. They will not depend on the immediate wind, but will depend on reactions to other environmental features which can still provide effective stimuli, such as fellow locusts or the sun. But the *tracks* of the insects will be biased more and more down-wind as the wind speed increases. If we enter a vertical line *MM* in figure 13*C*, where the wind speed is equal to the locusts' maximum air speed, then to the right of this line all tracks must be more or less down-wind.

A complication that arises in fixing the position of the maximum compensatory height is that the locusts' own air speed is a finite quantity which is added to the wind speed during down-wind flight and subtracted during up-wind flight. With a given locust air speed and wind speed, the ground speed will therefore be higher for down-wind than for up-wind fliers, so that the maximum compensatory height will also be higher for the down-wind fliers, other things being equal. On the other hand, for compensatory responses to be evoked, the front-to-back image movement which down-wind fliers experience must be considerably faster than the back-to-front image movement which up-wind fliers experience when they lose headway in strong winds. On this count, the maximum compensatory height will be higher for up-wind than for down-wind fliers. As a first approximation we shall assume these two opposite biases balance, and not complicate the diagrams by postulating different maximum compensatory heights for up-wind and down-wind fliers.

Now let us turn to the region below the line *KLJ*, in which the locusts are subjected to effective optomotor stimulation. Here the critical wind speed, which equals the locusts' maximum air speed, separates two regions in which not only the tracks, but also the effective responses of the locusts must differ. In the region to the right of *M*, bounded by *NMPLJ*, the locusts cannot progress directly into wind and will therefore turn more or less down-wind, so long, of course, as they remain air-borne. In the region to the left of *M*, bounded by *KPMO*, the locusts can progress directly into wind and will, if there is enough wind, set course against it, according to the theory (pp. 210–211); again, of course, so long as they remain air-borne. Flying on up-wind courses to the left of *M*, and down-wind to the right of *M*, are therefore entered as the characteristic *tendencies* in figure 13*D*.

The situation will be further differentiated within each region (figure 13*E*). In the upper part of *NMPLJ*, near the line *PL*, turning down-wind will be a completely successful compensatory response. The locusts there will be high enough not to experience too great a retinal velocity even when the wind speed is added to their own air speed. They will be able to fly both at their preferred air speed and with their preferred retinal velocity, so that under these height-wind conditions down-wind flight can become established as a level, steady course. Lower down, the retinal velocity will be too high in down-wind flight, leading to a reduction of air speed and, since this departure from the preferred air speed will evoke further compensation, to climbing until the retinal velocity falls to the preferred value at the preferred air speed. No stable combination of height, air speed and course seems possible in this region.

In the right-hand part of *KPMO*, near the line *PM*, up-wind flight will be very persistent, but cannot be entirely stable because it involves raising the air speed above the preferred value, and even so the retinal velocity will often be below that preferred, especially for fliers up near the line *KP*. Descent will raise the retinal velocity, but periodic rests may be the only adequate compensation for the high air speed necessary in these conditions. In lower wind speeds, somewhat below the insect's preferred air speed, up-wind flight can become established as a level, steady course. But as we pass into the region of very weak wind close to the ground, the wind's contribution to the insect's retinal velocity becomes eventually insignificant, relative to the part played by the insect's own air speed and course. The locusts' behaviour will no longer be appreciably affected by the wind.

At the same time, since the insects are very near the ground in this region *QKRO*, merely flying at their preferred air speed will itself create a retinal velocity in excess of that preferred. Reduction of air speed would lead to further compensation, but a successful response will be to climb. The height to which the insect must climb will decrease with the wind speed as indicated by the line *KR*. When the wind speed is negligibly small, near *QO*, the maximum compensatory height will now depend solely on the insect's air speed. It will be virtually independent of wind speed; hence the line *QK* is drawn horizontally.

The optomotor theory is not new in principle and assumes a fairly simple set of interdependent reactions. But it is abundantly clear that this theory, so far from leading one to expect some simple, fixed relation between wind direction and locust flight direction, provides the basis for a pattern of behaviour in the field which is decidedly complex and fluid, even when treated schematically as above. Before considering the actual field observations some further complications likely to occur in the field must be mentioned.

Even over a level plain, wind speed is not uniform. As one approaches the ground, the influence of friction becomes increasingly great, so that the wind speed becomes progressively lower. That is to say, in following the hypothetical behaviour of a locust rising from the ground, it would be wrong to read vertically up the diagram (figure 13*E*). The conditions experienced by a locust in climbing flight would be represented by a series of points on a line inclined upwards and to the right. Consequently it would be theoretically possible to see individual locusts behaving in the following way at one moment, but at different heights: fairly near the ground, in stable up-wind orientation; higher, oriented up-wind at increased air speed; higher, in the region where no stable orientation is to be expected; higher still, in stable orientation down-wind; and higher still, totally unrespon-

sive to the wind. Such a confused picture would nevertheless be entirely consistent with the optomotor hypothesis.

Moreover, the wind is at all times irregular in structure and often distinctly gusty, whereas the behaviour indicated in each part of figure 13 *E* assumes a steady state. Hence instantaneous field records of locust courses occurring in conjunction with particular wind speeds and directions cannot be expected to conform fully to the hypothesis, because the immediately previous wind speed and direction of the locusts recorded will have been different. This will apply especially to higher fliers.

Finally, it should be noted that quite different types of compensatory responses may intervene when optomotor responses to wind are weak or not evoked at all. For example, it is conceivable that a locust, having had an up-wind orientation imposed on it while near the ground and having at the same time established a light-compass orientation to the sun, will retain this after climbing to greater heights, where optomotor responses to the ground would not occur. Again, if a deep swarm is flying up-wind, the locusts near the ground being subject to strong optomotor responses to ground movement and taking up the consequent orientation, the whole swarm might retain a stable up-wind orientation through gregarious alinement. This seems especially likely if there is vertical circulation in the swarm, as there often is. These other types of compensatory response would therefore be capable of perpetuating orientations imposed by the wind after the insects had ceased to respond to the wind itself, for example, when the wind dropped below the minimum compensatory speed for the given height, or the locusts rose to above the maximum compensatory height for the given wind. Finally, and perhaps most important, responses to stimuli quite unconnected with the wind may dominate the insects' behaviour, even in circumstances when clear wind responses are expected theoretically. All such effects would make analysis of the wind's own optomotor effects doubly difficult in the field.

How far, nevertheless, do the field observations conform with the optomotor hypothesis of behaviour in relation to wind speed and height? The records refer to locusts flying fairly near the ground, of necessity, so that the eventual complete disappearance of wind responses at some height above the ground, assumed by the hypothesis, remains unconfirmed. The existence of a maximum compensatory height due to failure to resolve the elements in the background pattern is, however, suggested by the failure of responses among locusts *over water*, by contrast with their behaviour at the same height and in the same wind over nearby land (pp. 192–193 and 208). In the field, where, of course, the wind speed varies all the time, one would not expect to see a constant failure of responses above any particular level, but would expect rather to find a tendency for responsiveness to decrease with height. Thus, the existence of a maximum compensatory height, due to the apparent ground speed being too low even when the background pattern is resolvable, is in fact suggested by the observations that stronger winds were required to evoke responses from higher than from lower fliers (pp. 177, 179 and 185). The same observations suggest that insufficient retinal velocity, rather than the indistinctness of the background pattern, was what usually set the height limit to optomotor responses over land.

The numerical data summarized in figure 11 (p. 191) further support the supposition of responsiveness decreasing with height, but increasing with wind speed at a given height. The preponderance of up-wind courses was greater below than above 8 m. in winds up to

4 m./sec., and was greater in winds of 1 to <4 m./sec. than of less than 1 m./sec. In winds of 1 to <4 m./sec. the preference was sharper even over 8 m. than it was in winds of less than 1 m./sec. below 8 m.

The smaller proportion of up-wind courses among higher fliers was not merely due to the wind speed increasing from the ground upwards, making it more difficult for insects farther from the ground to make progress against the wind. What happened in winds of 4 to 7 m./sec., against which progress definitely was difficult, can be seen in the third lower diagram in figure 11; a preference for down-wind courses (as against across-wind ones) was added to the preference for up-wind courses. But in winds of less than 4 m./sec., there was no down-wind preference among higher fliers, which nevertheless showed a weaker up-wind preference than did lower fliers. This was evident even when the wind speed near the ground was less than 1 m./sec. and the ground was free of obstructions. The wind 8 m. above such ground could hardly reach 4 m./sec. when it was less than 1 m./sec. near the ground.

The fact that the data for winds of 4 to 7 m./sec. in figure 11 show a more clearly defined orientation preference among higher fliers than among lower ones does not mean that the lower fliers were less responsive. When watched continuously the lower fliers always seemed to be more responsive, but in these strong and gusty winds their responses were variable and did not result in steady flying in any one direction.

If responsiveness did decrease with height but increased with wind speed, as required by the hypothesis, what of the responses themselves? The collected records in figure 11 and the continuous observations figure 11 fairly reflects, show the up-wind preference in more moderate winds and down-wind preference among higher fliers in stronger wind, which are expected on the hypothesis. No down-wind *preference* is shown among the records for lower fliers in stronger winds, but the postulated tendency to turn down-wind was observed, and the general instability of behaviour under these height-wind conditions also accords with the hypothesis. The postulated tendency for up-wind fliers to descend and even settle when the wind speed increased to around their air speed was unmistakably observed.

A noticeable feature of the observed behaviour which is not expected on the hypothesis was the tendency of fliers caught in winds of 4 or more m./sec. to descend also. Hypothetically, ascent rather than descent is expected under such conditions, and the observations demand closer examination. In most cases when such descents were definitely observed the locusts had been progressing against less strong wind, had then been caught by a gust and had descended before turning round. Such descents are in accordance with the hypothesis, for as long as the insect retains its up-wind orientation and makes even a little headway, descent will raise the front-to-back retinal velocity toward that preferred, even if the wind speed is the same at the lower level. Often the wind speed will be less nearer the ground, and descent will then enable the insect to prevent image movement from back to front and increase its rate from front to back, with less effort. Ascent would have the opposite effects, still further reducing the rate of front-to-back image movement and increasing the likelihood of actual back-to-front movement. The conflict between observation and hypothesis here is more apparent than real, *fluctuating* wind conditions having been left out of account in the hypothesis as presented. Strictly speaking, locusts descending while holding their ground facing up-wind, and are in conditions to the left, not to the right of *M* in figure 13*E* (p. 213).

The situation becomes rather different if the locust has already reoriented down-wind as

a compensatory response. Such fliers, it is true, often turned up-wind again before descending and always did so before actually settling. But what of descents made while still oriented down-wind? When the locust is high the rate of front-to-back image movement may be less than that preferred, and descent to an intermediate level will increase the rate to the preferred value. But low-flying locusts, having been turned down-wind by a gust, will at once experience excessively fast front-to-back image movement and descent will make it even faster. Ascent would be expected on the optomotor theory, yet such ascents were rarely observed. Possibly that was because locusts were rarely seen in winds which were strong enough, and remained so for long enough near the ground, to prevent the down-wind fliers there from turning up-wind again and *then* descending, before an ascent while still oriented down-wind became the only successful form of compensation left to them.

It should be emphasized that while low, down-wind flying locusts were never seen to ascend, except in a gale, it is not as certain that they definitely descended, as it is that up-wind fliers and higher down-wind fliers definitely descended, in strong wind. Low, down-wind fliers passed the observer quickly, and it was not easy to follow the individual by eye and distinguish its descent from that of neighbouring up-wind fliers. The latter's descents were more certainly observed as they remained near the observer for longer.

The remaining part of the hypothesis, postulating a tendency to climb away from the ground when the wind speed falls well below the locusts' air speed, is consistent with the frequent observation that locusts not only descended in gusts but also rose actively into the air in lulls (pp. 178–181). If it seems at first strange that an active flier might need some inducement, such as an excessive retinal velocity, to make it rise away from the ground, that is only because it seems eminently 'logical' that it should rise, but this is not, of course, in any immediate sense a causal explanation of the behaviour.

Figure 12 (p. 192), which illustrates the orientation observations on semi-migrant locusts, shows, like figure 11 for full migrants, a predominance of up-wind courses among low-fliers with weak winds, but courses become random in direction at lower wind speeds than with migrants, which is to be expected from the lower air speed of semi-migrants. The more random courses of higher fliers at low wind speeds is again in accordance with expectation.

The field observations, so far as they go, are thus generally consistent with the elaborated hypothesis of optomotor behaviour and hence provide considerable support, short of direct proof, of the more general optomotor theory of reactions to wind.

We cannot at present assign any reliable values to the postulated preferred retinal velocity and preferred air speed of these locusts, but even very rough estimates might have some working value until superseded. If these two speeds are indeed preferred, one might be able to gain a rough idea of them from one's impression of 'average' behaviour. The preferred air speed might be put at about 3 m./sec., and the preferred retinal velocity at that experienced by a locust flying up-wind at about 6 m. above the ground with a ground speed of 3 m./sec. If so the preferred velocity will be experienced also at 2 m. high with a ground speed of 1 m./sec., 10 m. at 5 m./sec., and so on. In figure 13*E* (p. 191), *M* might fall at about 6 m./sec., *R* at 3 m./sec. and *Q* at, say, 6 m.

It is worth dwelling upon the new feature brought out by the locust observations which was not observed in the mosquito experiments and therefore not then considered in terms of compensatory reactions: the tendency to turn down-wind in strong winds.

The wind tunnel used in the mosquito experiments was so small that the insects reached the floor and alighted almost at once when unable to make headway against the wind. The sequence of events had they not been able to do so was not investigated. In the open air, when locusts were carried back by the wind and did not immediately settle, they turned away from their up-wind orientation. Sometimes they took up an across-wind course in which they were still able to make at least some headway over the ground, but if they stayed in the air they tended to turn right round and face due down-wind, even when some headway was being made in the across-wind orientation (pp. 184–193). Locusts in a gale, which seemed to stimulate continued flight with no possibility of making headway against the wind were oriented consistently down-wind (p. 183).

There are two questions here: first, why the locusts turn down-wind at all; and second, why down-wind courses predominated among higher fliers but not among lower fliers. An insect wavering to one side, with the onset of back-to-front image movement, would be able to reach an orientation where there was no longer any actual back-to-front image movement by perhaps quite a small turn. And, if hit by a gust in this position, it could eliminate the resultant back-to-front component in its image movement by quite a small increase of air speed, demanding less effort than the larger increase required while oriented directly into wind. But having made this turn, it would of course be drifting sideways and experiencing transverse image movement in a roughly up-wind direction. This should, on the theory advanced for up-wind orientation, evoke a compensatory turn up-wind. Given a wind speed higher than the insect's maximum air speed, however, such an up-wind turn could not be a successful compensatory response, for it would demand an increase of air speed which the insect cannot make. Yet what the insect actually does, turn down-wind, will not be a completely successful response either, for the front-to-back image movement it experiences while flying down-wind will be excessively fast. In fact, as was apparent in the field, such locusts are in an unstable condition.

It seems that, for a locust faced with this dilemma, direct front-to-back image movement at an excessive rate is more tolerable than transverse image movement at a somewhat less but still excessive rate, as well as more tolerable than even quite slow back-to-front movements, so that the down-wind orientation is taken up.

Two possibilities should be kept in mind with regard to this down-wind orientation. First, there must be an upper as well as a lower limit of retinal velocity at which optomotor responses fail. It may be that the image movement, being at its maximum rate in down-wind orientation, becomes so fast in a strong wind as to be blurred; a situation equivalent to no image movement and evoking no response. The actual turn down-wind might also be aided by the increasing blurring of all images experienced as the insect's translation over the ground becomes faster and faster, once it begins to turn. Also, some authors (see Kalmus 1949) have observed walking flies making optomotor responses, not only of the compensatory type in which the insect moves in the same direction as a moving background, but also responses in the opposite sense, in which the insect walks *against* the direction of the moving background. It is not clear what conditions are necessary for such responses to appear. Turning and moving with the wind is the visual equivalent for a flying insect of turning and moving against a moving background in still air. In both cases the insect moves against the direction of apparent background movement. It would be worth investigating whether,

when the insect can no longer make headway against the wind, that is, when it is in a situation where ordinary compensatory responses cannot be 'successful', this causes a switch-over from the first, compensatory type of optomotor reaction to the second, opposite type of optomotor reaction.

For higher fliers, the stability of down-wind courses was expected from the hypothetical analysis, because a locust can achieve its preferred retinal velocity and air speed while oriented down-wind in a strong wind while it be fairly high, but not if it be low. But to some extent the greater duration of down-wind courses among high-fliers could be attributed to the mere fact that they took longer to complete the other type of response to strong wind, descent (p. 192). The tendency to turn down-wind in excessive wind has less chance to show itself among low-fliers, for among them it is cut short by settling or by entry into a slower-moving air layer near the ground.

The optomotor theory in the literature. The optomotor theory of wind orientation has been discussed by Fraenkel (1932), de Lépiney (1928, 1933), Williams (1930, 1942, 1949), Gunn *et al.* (1948) and Waloff & Rainey (1951). None of these authors has, however, quoted observations with the accompanying information on both wind speed and height of flight which would help to decide for or against the optomotor theory. Fraenkel recognized that the necessary evidence was not yet available. He called, in particular, for information on wind orientation over a uniform substrate such as the sea (Fraenkel 1932, p. 205). Just this kind of evidence in favour of the optomotor theory of wind orientation is now available for locusts (pp. 192–193), but at that time Fraenkel could refer only to the fact that insects were nearly always reported as having crossed the sea with particular winds, and this kind of circumstantial evidence is also now available in detailed form for locusts (Waloff 1946*b*; Rainey & Waloff 1948). Fraenkel emphasized the difficulties facing any alternative theory which assumed a direct orienting action by the wind, and the absence of any need to create such a theory in view of the experimental evidence that an optical mechanism was concerned in the analogous case of orientation against a stream of water (rheotaxis).

De Lépiney (1928, 1933) mentions the hypothesis of wind orientation by optical compensatory responses to the apparent movement of the ground, but dismisses it along with several others. He does so on three grounds: that the course of the various swarms he saw remained very much the same for hours and days together while their tracks varied greatly according to the wind; that the eyes of locusts are not directed downwards; and that on close approach to the ground, and only then, do locusts appear to react to objects there. With regard to the last point, distinct reactions to particular objects are not under consideration here, but rather reactions to the apparent movement of the whole array of objects forming the visible substrate. With regard to the second point, de Lépiney's statement that the eyes are not directed downwards does not seem to be based on any published work. Vertical transverse sections, for example, have not been published for *Schistocerca*. The 'pseudo-pupil' of *Schistocerca* (Roonwal 1947) can be followed down in the transverse plane to within about 30° of the vertical, but the anatomical meaning of this phenomenon has yet to be determined with certainty.

De Lépiney's first objection does not seem justified by the observations he quotes. He mentions 50 m. as the maximum height at which he observed swarms flying, but does not say what was the normal height. If, for example, the swarms observed by him were flying

mainly over 10 m. above the ground and the winds were generally weak, then one would not expect optomotor responses to wind to occur. One would expect what he describes: tracks varying according to wind direction and strength, but course remaining relatively constant (figure 8*A* and *B*, p. 187), through the joint action of the light-compass reaction to the sun and gregarious inertia (p. 243). It is probable the winds were rather weak at the time of de Lépiney's observations, for they were made at a period (winter) when the whole migration trend is against the prevailing wind in North Africa.

Williams (1942) questioned whether the laboratory demonstration of wind orientation by visual means (Kennedy 1940) would have any bearing on behaviour in the field, for the experimental mosquitoes were at most only 10 cm. above the visible background, and the apparent movement would be much slower at normal flying heights outdoors.

The diminished rate of apparent movement resulting from merely increasing height is fully recognized in the hypothesis now put forward. Given an adequately patchy appearance of the ground, a given retinal velocity can be produced at any height, but the ground speed required will be proportional to the height. It is for this very reason that a locust becomes less restrained in its orientation and speed as its height increases (figure 13*B*, p. 213), without any change whatever in its compensatory behaviour. It may very well be that the ground is sometimes not adequately patchy (figure 13*A*); that appeared to be so as low as 5 m. in the case of the wavelets on a lake, but considerably higher over land (pp. 192–193). Although the figures given on p. 218 are very rough estimates, they do suggest there is no intrinsic difficulty in envisaging the wind as an important orienting influence acting via optical responses to apparent ground movement, in the field as well as in the laboratory.

Rather better estimates can be made for mosquitoes. It was found that mosquitoes began to show a noticeable preference in orientation, by ceasing altogether to fly against the direction of moving floor stripes, when the stripe movement exceeded about 0.15 m./sec. At considerably lower stripe speeds flight in this direction was already slow, wavering and less frequent than flight in the opposite direction. If we take 0.10 m./sec. as a generous estimate of the minimum stimulatory stripe speed for a mosquito flying against the stripes and 10 cm. above them, and if we take 0.15 m./sec. as the mosquito's air speed, then the minimum stimulatory ground speed will be 0.25 m./sec. If so, the minimum stimulatory ground speed will be 2.5 m./sec. at 1 m. above the stripes, 25 m./sec. at 10 m., and so on. Hence the maximum height at which the mosquito will receive effective optomotor stimulation, in a 1 m./sec. wind, will be $(1 + 0.15)/2.5 = 0.46$ m.; in a 10 m./sec. wind it will be 4.6 m., and so on. These estimates of the maximum compensatory height for mosquitoes seem in fact too low, for the writer has observed various midges, mosquitoes and may-flies swarming up to 2 m. away from the nearest fixed object and maintaining their position against the gentlest breezes, by closely regulating their air speed and orientation.

In place of the optomotor theory of behaviour in wind, Williams (1930), concerned primarily with butterfly migration, advanced the suggestion that migrants are guided by an innate sense of direction regardless of the wind. Without details as to wind speed and height of flight the data on butterfly directions cannot be compared with the locust data, but Williams has applied his suggestion to other features of behaviour in wind for which comparable locust observations are available. He quotes two butterfly observers as recording an inverse relation between wind strength and height of flight, the insects coming low when

the wind was strong, but rising in little or no wind. The present author has observed the same behaviour, not only in locusts (pp. 178–182) but in many insects, including butterflies. Williams concluded from the observations he quoted, together with others in which high-flying butterflies were seen oriented with the wind but low-flying ones against it, that ‘butterflies may take advantage of a following wind by rising higher, and avoid a contrary wind by keeping close to the ground; but that, independent of any wind direction which may occur at the time, there is a direction in which they are urged to go, and they make every effort to keep to it’. Here Williams seems to be doing what he describes in another place in the same book as ‘appealing to internal unknown or little known forces—thereby leaving the question quite unsettled’. To speak of insects ‘taking advantage’ of a given wind direction is to assume that the insects anticipate which winds will be to their advantage and which will not. The optomotor theory demands considerably less of the insects, and will account, as set out above, both for the changes of height with changes of wind speed and for the changes of wind orientation with change of height.

Gunn *et al.* (1948, p. 46) have brought forward a particular form of the optomotor theory of wind orientation which is embodied in their expression ‘the forbidden course’. Observing that locusts did not maintain steady flight while being carried backwards by the wind, however small the backward component in their ground speed might be, but did fly on a track nearly at right angles to their course, the authors suggested that a course which would lead to any degree of backward drift was ‘forbidden’ for, that is to say avoided by, the locusts. This theory fits some of the facts and enabled Gunn *et al.* to narrow down the possible range of courses along which swarms could have flown in given wind conditions. But the optomotor responses of flying locusts involve more than the mere avoidance of backward drift. Figure 11 (p. 191) illustrates the finding that locusts have a preference for up-wind orientation even when winds are gentle enough for there to be no risk of backward drift while so oriented. The same applies to mosquitoes (see pp. 209 and 221). Hence the suggestion that up-wind orientation was due to compensation of *transverse* image movement even before there is any back-to-front component in that movement (p. 210). Such compensatory reactions will, naturally, only occur provided, as with other kinds of image movement, that the rate is neither too low nor too high for the movement to be distinguished. The significance of the ‘forbidden course’ appears to be that, when a back-to-front component does develop, the insect begins to react in a new way, changing over to a different kind of compensatory response now that the old one has failed to maintain the preferred direction of image movement. It may descend and even settle; or it turns, now tolerating transverse image movement, and thereby avoiding not only the ‘forbidden’ back-to-front image movement, but equally the ‘forbidden’ (excessive) air speed which continued progress directly into wind would demand (pp. 184 and 219).

Waloff & Rainey (1951) consider that the preference for roughly up-wind courses at wind speeds up to 3 m./sec. (see p. 205), could be accounted for satisfactorily without invoking any optomotor hypothesis. They suggest that it is due to the mere continuance after take-off, of the up-wind orientation assumed before take-off, when the locust is in a position to respond to the mechanical pressure of the wind (p. 208). The continuance of a mechanically stimulated orientation may well contribute to the frequent occurrence of up-wind courses among low fliers, especially in ‘rolling’ swarms. But it is hardly a sufficient

explanation, because fliers are also observed very regularly to have assumed that orientation just prior to alighting, whatever their previous course may have been (p. 185).

Waloff & Rainey devoted more attention to possible optomotor effects, when analyzing their 'snapshot' readings in relation to very short-term wind fluctuations. They examined two possible ways in which the locusts' courses might be adjusted to such fluctuations: so as to maintain either a constant angle between course and wind, or a constant direction of displacement over the ground. In the event, the analysis demonstrated neither of these kinds of constancy. It seems very doubtful whether a limited number of 'snapshot' readings from a wide range of heights in fluctuating wind, could, by themselves, throw any light on the situation. The authors did not indeed exclude the possibility of demonstrating an effect of rapid wind changes on the orientation of fliers, with improved techniques; in any case there are grounds (pp. 196 and 242) for expecting such effects to be less marked than the effects of longer-term wind changes.

Conclusions. It will be as well to recapitulate the tentative conclusions now reached concerning the complex matter of wind and migratory behaviour, with special reference to the optomotor theory and the hypothesis elaborated from it. The conclusions will be given under the headings of taking-off and settling, speed of flight, height of flight, and direction of flight, but these aspects of behaviour are in practice integrated, in such a way as to create a strong presumption that migrant locusts have both a preferred retinal velocity and a preferred air speed.

Taking-off and settling. Strong wind has a suppressive effect on taking-off and on flight near the ground, but less effect on flight well above the ground. Fliers near the ground are caused to settle by gusts, while taking-off occurs in lulls, so that gusty winds may produce a resultant down-wind movement. These facts are consistent with the optomotor theory.

Speed of flight. The cruising air speed of *Schistocerca* is in the region of 3 m./sec., but when flying close to the ground against a wind of varying speed the locusts seem to stabilize their ground speed by varying their air speed which may then reach 5 m./sec. or more for short periods at least. Farther away from the ground, air speed seems less influenced by wind speed, and at sufficient height is presumed to be entirely uninfluenced, unless temporarily in very turbulent air. These conclusions are also consistent with the optomotor theory, but there is an urgent need for further measurements of air speeds in known conditions.

Height of flight, among low-fliers, depends on the wind speed in much the same way as taking-off and settling; locusts ascend somewhat in lulls and descend in gusts. This accords with the optomotor hypothesis of a preferred retinal velocity attainable at a height which decreases with the wind speed. Higher fliers are less responsive to wind-speed changes in accordance with the hypothesis of a maximum compensatory height above which no optomotor responses occur, this height increasing with the wind speed. The optomotor effect of height is quite unconnected with the fact that wind speed generally increases with height, a fact which in no way alters the hypothesis but which does complicate its detailed investigation and application. The optomotor effect is geometrical, varying directly with height, whereas the wind speed does not change so fast with height. But since the wind speed does increase somewhat with height, locusts climbing in moderate winds will tend to suffer backward drift, compensated by reducing height, with the result that sustained flight in

moderate winds should be predominantly up-wind at low heights. This seems to fit the available data reasonably well and to agree with one's general impression, but more and more precise field measurements are required.

Direction of flight. In moderate winds near the ground locusts orient preferentially into wind. This preference becomes less marked higher up in the same wind or in weaker winds low down. It has already been mentioned that in moderate winds the vertical wind gradient would tend to encourage low flying up-wind. At wind speeds around the maximum speed at which the insects will fly they turn away from their up-wind orientation and tend to fly oriented down-wind, especially if fairly high. But in this respect, too, they become eventually less responsive at sufficient height. All this accords with the optomotor hypothesis which carries the further implication that orientations will be quite unaffected by the wind direction above the maximum compensatory height. But further observations are required to establish these conclusions, to express them in terms of actual wind speeds and heights and to determine the preferred retinal velocity and air speed.

If these are the conclusions reached by considering the behaviour of an isolated locust, the situation becomes somewhat different with a dense swarm of locusts extending from the ground upwards, for we have to reckon with the reaction of one locust to another. In moderate winds the low-flying locusts should orientate up-wind and, even if the high-flying ones are above the maximum compensatory height, they should tend because of gregarious behaviour to fly with their fellows below and therefore up-wind too. This tendency should be reinforced by the vertical circulation which takes place within a swarm and the stabilizing effect of the sun-compass reaction, although with very deep swarms the connexion may very well break down.

This tendency to up-wind flight by large swarms is likely to be modified when the upper locusts are above the maximum compensatory height, except when the wind reaches the upper limit of air speed. The upper locusts are then expected to swing round and fly down-wind, giving the not unfamiliar picture of a shearing swarm, with the lower layer progressing slowly up-wind and the upper layer scudding down-wind, and with interchange taking place between the layers as gusts come and go.

Gregariousness

The evidence of gregariousness. Evidence that mutual stimulation among swarm adults provides some of the impetus for migration, and is partly responsible for the parallelism of movement within the swarm, has been quoted earlier (pp. 193–195). The general grounds for regarding gregariousness as primarily responsible for the cohesion of swarms have been stated by Gunn *et al.* (1948):

‘When large numbers of individuals come together and remain together for long periods while moving through a complex and highly variable series of natural situations with no discoverable common factor other than the crowd itself, one is left with a strong impression that the animals are bound together by reactions to one another.’

It might seem unnecessary to stress the real existence of gregarious behaviour among locusts. But it is necessary to stress it, since Chauvin (1947) has questioned the existence of both mutual activation and mutual attraction. In his view the cohesion of marching hopper bands could be due entirely to their following parallel paths through independent but

identical responses to some (unknown) external directing agency. Here it is enough merely to recall the frequent occurrence of gregarious re-alignment (p. 194). Temporary dispersals and deviations occur too often for the cohesion of migrating locusts to be accounted for by such externally directed, parallel progression.

The cohesion of stationary bands Chauvin would again ascribe entirely to independent but identical responses to external stimuli, especially temperature. It is recognized that individual responses to topographical temperature differences help to keep stationary bands and swarms together. But gregariousness also contributes, for it has been found that positions close to but *not* occupied by basking hoppers do not differ detectably in any respect, including temperature and draughtiness, from the adjacent positions occupied by bands (Kennedy 1939, p. 519; Pielou 1948). Writing of *Nomadacris septemfasciata* hoppers on dense tall grass, Pielou says:

‘The tendency to form dense clusters, in which hopper is often on top of hopper, when there is plenty of grass around for all, is a striking example of gregarious behaviour.’

Events during the launching process of swarms (p. 193) provide perhaps the best evidence that mutual stimulation contributes some of the impetus for migration. On this point, too, the conclusions on adults are supported by observations on hoppers. Pielou (1948) describes how an initial slight disturbance sets up a cumulative chain reaction in small hopper bands of *N. septemfasciata*, and may lead to the whole bandlet moving off in one direction. He goes on:

‘Within four or five seconds this outburst of activity dies down but, before finally disappearing, may build up again and repeat itself in a striking manner without any further obvious external disturbance’.

The writer has observed the same sequence of events in small bands of *Schistocerca* hoppers.

Pielou's hopper bandlets were evidently in an unstable condition: not normally migrant, but easily ‘catalyzed’ into intense, *self*-sustained activity by external stimuli. He emphasizes that his bands were small and that larger, denser bands of the same species migrate more actively. One is strongly tempted to conclude from this work, and from the more quantitative work of Smit (1939) on the critical density for migration by *Locusta pardalina* hoppers, that the same hoppers would migrate more actively in large dense bands than in smaller, less dense bands. Clark (1950) has actually recorded such differences in *Chortoicetes terminifera* bands, and it has been observed that *gregaria* Desert Locust hoppers migrate less persistently when isolated than when in bands (Fraenkel 1929; Kennedy 1939).

There is a need for more field and laboratory experiments on this point, using both hoppers and adults known to have had exactly the same history up to the moment of the experiment, and along the lines suggested by Gunn *et al.* (1948, p. 24).

As far as adults are concerned, there is some rather inconclusive additional evidence of a difference between the behaviour of migrants in swarms and migrants on their own. During the summer of 1941 when swarms were seen by day emigrating westwards from the Anglo-Egyptian Sudan, numerous isolated yellow migrants were seen at Geneina, Darfur, flying west round the time of full moon in several successive months, and these individual flights were seen only at night (personal communication from Mr Bampffield, British Overseas Airways Corporation). Similarly, Predtechensky (1935*b*) observed isolated *gregaria*

individuals flying high late at night, at a time when swarms were flying by day and settled at night.

The evidence of gregarious behaviour in locusts seems to be conclusive, but it must be emphasized that migrants will fly steadily onward following parallel courses even when they are not subject to at any rate frequent stimulation from one another (p. 194 and 195).

Gregarious reactions. Mutual visual, olfactory, tactile, auditory, humidity and temperature reactions have all been suggested at one time or another as the basis of gregarious behaviour. Humidity was suggested by Chauvin (1941) on very doubtful evidence, and seems most improbable not only because it is unspecific, but also because there is experimental evidence that *Locusta* hoppers collect in the driest places available, other things being equal (Kennedy 1937). Temperature, in the form of responses to the heat radiated from the sun-warmed black bodies of fellow-hoppers, was suggested by Shumakov (1940) as a possible aid to the formation of basking bands. This seems more likely but has not been tested.

Certain field observations on hoppers led de Lépiney (1933) to suggest olfactory responses were of considerable importance in band cohesion. But Volkonsky (1942) stated that such responses, while important during gregarization, were reduced to a minor role or even disappeared when fully *gregaria* locusts had been produced. Tactile responses, on the other hand, are plainly seen among roosting and basking adults, and in the jostling that goes on at times in both stationary and marching hopper bands as a number of authors have reported.

None of these types of mutual stimulation can take us far toward understanding gregarious behaviour in migrating bands and swarms. The air-borne stimuli, humidity and smell, could not explain the gregarious responses of hoppers to fellows down-wind of them, and could hardly produce responses as rapid and precise as those observed. Thermal radiation and mechanical contact can affect only insects in very close proximity. Auditory and visual stimuli seem to be the only ones which would be capable of producing gregarious responses with the rapidity and precision, and over the distances, observed among migrant locusts in the field.

Observations and experiments in the field led Vayssi re (1921) to suggest that locusts respond selectively to the air vibrations set up by their fellow-locusts, but seemingly clear evidence of this has been confused by contradictory field observations (Uvarov 1928; de Lépiney 1928, 1930; Williams 1933). In the laboratory, Pumphrey (1940) established the range of frequencies to which the tympanal organs of locusts respond, and their discriminatory responses to modulations of the basic frequencies. He showed, moreover, that these paired organs are capable of discriminating the direction from which sounds come. Later (in a private communication he has kindly allowed me to quote) he reported that the sound emitted by one flying locust evoked a definite response from the tympanal organs of another, and suggested that auditory reactions could serve as a means of maintaining swarm (and perhaps band) cohesion. It is to be hoped these promising developments will be followed up by field experiments, for auditory reactions might play an important part not only in inter-attraction but also in mutual activation among swarm members, as well as making it easier to understand the cohesion of swarms migrating by night. To man, there is, for example, an extended and dramatic swish of wings as the growing flocks of locusts sweep over at mass departure, and this sound might contribute toward bringing still-settled locusts into the air during the climactic last minutes of the swarm-launching process.

On present evidence, however, first place among the agents of gregarious behaviour must be given to vision (Uvarov 1928; Kennedy 1939; Volkonsky 1942). Chauvin (1941) implies that the present writer (1939) regarded the visual attraction of hoppers to shrubs as the main evidence that the inter-attraction between hoppers was also visual. That was only a minor point. Evidence for the visual nature of inter-attraction comes from the sensitivity of locusts to all kinds of visual stimuli, especially movement, from the dense, sharp front shown by some marching bands, and from the speed and precision of the responses of one individual to another and their independence of air movement.

Volkonsky (1942) satisfied himself that the inter-attraction of *gregaria* was visual, by field experiments which he did not, unfortunately, describe. He attributed it to a

‘réaction visuelle de réorientation qui consiste à ramener l’image d’individus frères dans la partie antérieure de l’œil composé’.

He distinguished this reaction from the one responsible for parallel marching:

‘Une stimulation opto-motrice entre individus marchant parallèlement et qui ne persiste que tant que l’image stimulante se trouve située dans la moitié antérieure de l’œil composé.’

The cohesion of *gregaria* bands he attributed to the joint action of these two reactions:

‘Cette réaction visuelle de réorientation (particulière à la phase grégaire) s’ajoutant à la stimulation opto-motrice réciproque (déjà observée chez les *congregans*) permettrait d’expliquer la cohésion des bandes.’

This dual conception of gregarious reactions is expressed most clearly in his interpretation of marching:

‘L’errance apparaît ainsi comme l’extériorisation de stimulations motrices réciproques, contrebalancées par une inter-attraction des individus.’

At first sight marching behaviour does certainly suggest there are two different reactions counter-balancing one another. But on close examination it is difficult to see a clear distinction between them; what we observe are two forms of expression of a common underlying reaction. The optomotor reaction is not, during marching, merely a means by which one insect makes another one move; it makes the other move in a certain direction, parallel with the first. It helps to prevent scattering and is in this sense an agent of inter-attraction. The present writer (1939, pp. 525–6) suggested previously that there was no fundamental distinction between the reactions involved in inter-attraction and parallel movement; nor, indeed, between them and the attraction of non-migrating locusts to conspicuous objects (p. 243). He would now add orientation to wind as another allied reaction. All these reactions appear to rest on the common foundation of optomotor (visual compensatory) responses. They differ in being evoked by different types and patterns of image movement and involve different forms and patterns of optomotor responses.

Not only is the basic response common to these different types of reaction. The different types of effective stimulus-situation involved also have something in common. They all have something exceptional, outstanding or novel about them. The reactions of an individual hopper to the movement of a man’s arm show this same feature. If he holds his arm out but

stationary, or moves it very slowly, the insect is unaffected. If he moves it more rapidly, the insect may pause and 'peer' at him. If he moves it yet more rapidly, the insect hops wildly. Similarly, in wind orientation, the insects do not make optomotor responses to *any* background image movement, such as the movement of images from front to back which is the normal and inevitable consequence of the insect's own movement. The optomotor responses appear when the retinal velocity is novel in the sense of being a departure from that which the insect prefers. In attraction to vegetation the insects do not turn toward *any* object along their path, "à ramener l'image dans la partie antérieure de l'œil", but only toward outstanding objects like isolated shrubs.

Among *moving* fellows, as in migrating hopper bands and flying swarms, the pattern of optomotor responses seems to be governed in much the same way as their pattern in wind is governed. Image-movement from front to back at a moderate rate, as in the eyes of one locust overtaking its neighbour, evokes no compensatory response in the overtaker; it does not at once drop back to its previous position relative to its neighbour. But when the neighbour is coming in the opposite direction, so that the image movement from front to back is at an excessively high rate, the locust does respond, by turning and following its neighbour, as seen during 'gregarious reversal' (p. 229). Again, when the image-movement passes from back to front in the eye owing to being overtaken by a neighbour, this too is compensated; it is not a consequence of the locust's own exertions. It provokes a powerful optomotor response, which gives the impression of an attempt to catch up with the intruder. Back-to-front movement of background images owing to failure to make headway against wind seems to be compensated in much the same way, by an increase of pace.

As far as the purely optical reactions are concerned, there seems to be no essential difference between those responsible for mutual attraction as seen most clearly during convergent movement into stationary bands, and those responsible for parallel movement in marching bands. What differs in the two situations is the behaviour pattern shown by the band or swarm as a whole.

When most of the hoppers are stationary, the neighbour-image-movement experienced by a moving hopper is due largely to its own movement. The moving individual's compensatory responses to such image-movement bring the image concerned to the front of its eye, for only in that position will the image cease to shift about on the eye while the insect moves, as in what Kalmus (1937, 1949) has called photo-horotaxis. Isolated hoppers are thereby directed into the main body from any point outside it. When, on the contrary, the majority of insects are moving, the image-movement experienced by any one of them is due largely to the movements of its neighbours and not of itself. A hopper making a compensatory response to the movement of a neighbour crossing its path must turn after, that is in pursuit of, its neighbour. It may be left behind before becoming fully alined with its neighbour, and cease to respond to it. It then pauses, or continues on its own course until it sees and responds to a newcomer, and so on.

That sort of sequence is seen early in the launching process of a hopper band or adult swarm in the morning, or again when two bands or swarms meet at an angle. But when a band or swarm has launched on migration, gross deviations between individual paths are less often seen. The parallelism may then be due partly to the sun-compass-reaction. But

gregarious responses still appear wherever the insects are crowded and each individual is bombarded with stimuli from its neighbours. Movements of one individual toward a neighbour seen on its flank, and so across the main direction of the mass, simply do not have time to develop. The neighbour shoots ahead, followed by others, and the compensatory movement becomes a pursuit in line with the mass before it has developed into a traverse across the mass. Forward movement in line with the mass, originating early in the launching process as a pursuit of neighbours, evolves into a preoccupation with simply keeping up with neighbours on either side in the fully migrating band or swarm. Compensatory responses of this type perpetuate parallel movement and generate gregarious inertia.

The continuing occurrence of active gregarious responses during the process of swarm migration shows itself in the abruptness of 'gregarious reversal' in wind (p. 194). This term was applied to the remarkably well-synchronized change of course by members of dense swarms, from up-wind to down-wind in gusts and back to up-wind in lulls. Its effect seemed to be to impose due down-wind courses on locusts which, when less dense, merely turned from up-wind to some across-wind course when hit by a gust. Gregarious reversal seemed to depend on the fact that locusts losing headway or turning aside from their up-wind course began at once to drop backwards relative to their fellows still making headway into wind, thus stimulating the latter to turn down-wind after them until all were flying in parallel down-wind.

The differences between the tracks of neighbouring fliers, which are here assumed to be the starting point for gregarious reversal in gusts, could come about in at least two ways. First, it may be assumed that individuals differ in respect of the timing and strength of the responses governing their air speed and course. Secondly, the tracks of individuals will differ also because the wind itself is not a smooth current, least of all during the onset of a gust. This is apparent from the findings of Giblett (1932), who has been quoted already in part (p. 207) to show that the large differences of velocity found in wind were unlikely to affect orientation. Within these large 'eddyies', however, there are much smaller eddyies which produce rapid, *randomly* directed oscillations in a wind-vane. Giblett writes (p. 47):

'The wind-vane has a tendency to oscillate very decidedly at certain times and at others to remain much more steady... A comparison of these points with the wind speed records show that the period of oscillation corresponds to a lull in the wind while the subsequent period of little oscillation corresponds to an increased velocity... the decrease of oscillation occurred some 20 seconds after the increase of speed. It would appear that during lulls in the wind and the initial stages of a gust there is a greater small-scale turbulence than after the establishment of the higher wind-speed.'

Locusts meeting a gust would experience a sudden increase in turbulence, which would change the locusts' positions in relation to one another by disarranging their tracks, even if their courses were at first unaltered. As an immediate consequence courses would also be thrown into confusion as each locust made compensation movements in response to the visible displacement of its neighbours. The sharp turbulence is over in about 20 sec. and the wind becomes smoother than it was before the gust, but remains stronger. With locusts now facing in all directions and some therefore being carried down-wind past the eyes of

others, and none able to progress due up-wind, a common down-wind course should be achieved rapidly.

Confusion among fliers at the onset of a gust was often observed, as was to be expected from the meteorologists' results. The confusion was greater among higher than among lower fliers. The reason for this may well be that locusts flying above the maximum compensatory height have no means of 'correcting' their disordered orientations other than gregarious influence from lower fliers and the light-compass-reaction to the sun. Fliers below the maximum compensatory height can readjust their orientation to the main wind direction quickly, between eddies or as they subside.

The contribution of gregariousness to migration. If gregariousness contributes to the impetus of the migrant swarm and is largely responsible for its cohesion and the parallel movement of its members, then it must be regarded as a very important component of migratory behaviour in swarming locusts. We may reasonably infer that the migration of these insects would be less persistent, if they did not move in compact, 'disciplined' armies. If they did not migrate in this way, be it noted, they would lose their uniquely catastrophic character as pests of crops.

Their migration starts with the act of *mass departure* as it has been called, that is, when a large collection of insects not only start persistent flying at the same time, but all do so in the same direction and keep together in a group. Whatever may influence it, mass departure is by its very nature a gregarious act; that is, it expresses a change in the relations between individuals. The change is in the direction of closer inter-dependence, and this leads to that striking change in the movement pattern of the whole mass, called mass departure. Mass departure is not a matter of individual behaviour.

This point is stressed here because Gunn *et al.* (1945, 1948) seem not to have taken it fully into account, although their study of the swarm launching process is the most thorough yet made. In one place (1948, p. 30) they did state that 'stream-away is essentially a mass phenomenon'. Nevertheless, the conclusion they first drew (1945) from their study of the various factors that might affect the time of mass departure was that it was 'not due to a metabolic effect of the body temperature, once that is high enough, but is a *reaction* to air temperature'. That is to say, the phenomenon was attributed to the direct action of temperature on individuals, rather than to an indirect effect, through the gregarious relations between individuals, on the movement-pattern of the mass.

In the later, full account of their observations, Gunn *et al.* (1948) granted that the air temperature might play a 'permissive' rather than a directly stimulating role in mass departure, but they left the whole question open, as a problem of balancing the quantitative importance of one factor against others, and said (p. 44): 'gregariousness may not in itself be a causal factor in migration, though it may very well be a modifying factor.' If, however, it be conceded that mass departure is by its very nature a gregarious act, then gregariousness is thereby conceded to be a causal factor in swarm migration, and there is an *a priori* case for the role of temperature and of other external influences being in fact permissive (see also pp. 236-238).

Each *gregaria* locust is an individual capable of independent activity and differing somewhat from its fellows in its responsiveness to external stimuli, including those from its fellows; and yet it is also a swarm member, capable of the closest integration into a larger

unit of its fellows because its anatomy and physiology are such that it responds similarly to, and itself provides, the same types of stimuli as they do. The actual behaviour of an individual may be dominated by either one of these two sides of its nature, according to how much stimulation it is receiving from fellow-locusts. And the gross movement-pattern shown by a mass of locusts depends on which tendency is uppermost in the individuals composing it. Since other, extrinsic factors can influence the amount of stimulation the individual receives from its fellows, these factors exert a real, although indirect, effect on the gross movement-pattern shown by the mass.

The whole launching process may be visualized in this light, on the working assumption that the air temperature acts permissively, through the internal temperature of the locusts, and in the following, necessarily rather schematic way.

We start with a mere *assembly* of individuals, crowded but inert and in no immediate sense gregarious, which are then slowly brought into activity by the rising temperature. Up to and through the phase of vol-planing and hopping flights the locusts' influence upon one another is limited almost entirely to mechanical contacts. Flying locusts appear to have a negligible effect on other locusts resting or flying. The fliers are too isolated and their flights too brief, and the others are not yet sufficiently responsive. As fliers become more numerous and their flights lengthen, the movement pattern of the mass enters the 'milling' phase. Obvious mutual stimulation, of resting locust by flier and of flier by flier, becomes quite frequent. The locusts still behave mainly as independent individuals, but increasingly supply and respond to the specific stimuli which make them potential swarm members. But as no more than two or three individuals are involved in any one exchange of stimuli and then only momentarily, they only deflect one another. Directions generally are chaotic; hence the term 'milling'.

As they get warmer more locusts fly and fliers stay in the air still longer, permitting gregarious and extrinsic orienting influences to create the rudiments of order. The individual is now exposed to successions of stimuli from neighbours, and parallelism appears. Groups are formed in the air, and gregarious re-alignment is increasingly of group by group, or of group by external agency (gregarious reversal in wind). We now have 'surging'. But the groups are local and transient and follow divergent and inconstant directions. Any given individual displays fully gregarious behaviour only in brief spells which are terminated when it flies out of its group, or when loss of heat to the air stops its flying and in that way cuts it off from the group. While resting it reverts to its individual status, or regains a different form of gregarious status as a member of a basking group, more local and less fluid. During milling and surging the whole mass of insects is more than an assembly, but less than a swarm; it is a *mob*.

Eventually it becomes warm enough for locusts that take off to be able to fly on indefinitely. A new situation now exists, for it has become possible for all the locusts in the mass to be in the air together. Mass departure has become possible. In this limited sense the rising temperature causes the mass departure. But the newly created possibility of mass departure cannot be translated into actuality until all the locusts get into the air.

In fact, as was mentioned, taking off does increase decidedly at this point. There is no evidence for and no need to postulate any acceleration in the direct effect of temperature on taking off, or any nervous reaction to the air temperature occurring at this time but not

before. On the contrary, the break in the rising activity curve and the climax of mass departure can be brought about by an unbroken rise in temperature-regulated activity among physiologically quite heterogeneous insects, because there occurs a marked strengthening of the gregarious component in the behaviour of all the individuals in the mass.

As soon as flights are no longer curtailed by the coolness of the air the number of fliers in the air rises steeply. It would do so, owing to the lengthening of flights, even if the frequency of take-offs remained unchanged. But, in addition, the growing masses of fliers in the air stimulate taking off by flock after flock of those still settled, until the entire mass is in the air. The mass is now more or less continuous, the groups having fused. Gregarious re-alignment can spread right through it. This creates a common direction among all the individuals, with gregarious inertia now a property of the whole; gregariousness reaches its fullest expression. This in turn leads to displacement of the whole. The mass is no longer a mob. It has become a swarm; and that, essentially, is what enables and obliges it to depart.

To sum up: gregariousness plays a significant part in migration, being one source of its 'momentum'. Gregariousness affects also the direction of migration, by generating gregarious inertia. This may be an important direction-stabilizing agency, especially if combined with a sun-compass-reaction.

Air and body temperatures

Flight activity. Much remains obscure concerning the effects of temperature on locust activity, but there is now enough information to form an opinion on the question of whether swarm migration is reflexly provoked or, in the main, merely released by it. The question touches on the fundamental nature of migratory behaviour, and has been answered in both ways. The suggestion that migration is provoked by temperature has been made at least twice, in different forms, flight being attributed at one time to over-heating, and more recently to a reflex acting through special air-temperature receptors.

Hussein's (1937) laboratory work on temperature and locust activity led Uvarov (1937*a*, 1937*b*) at one time to the conclusion that:

'Mass movements of hoppers and flights of adults, which are so characteristic of locusts, are not normal movements, but are caused by excessive temperatures. These movements are definitely due to external factors and they continue only as long as the conditions remain unfavourable' (Uvarov 1937*b*, p. iv).

Since then, Uvarov (1947, p. 16) has taken up the opposite view:

'As a rule, if temperatures are above a certain moderate level, gregarious locusts are more likely to be in flight than at rest. Flying with them may be regarded as a normal state, and rest is enforced by environmental conditions.'

The evidence undoubtedly favours this latter view, rest being presumably sometimes enforced not only by external but also by internal conditions. Since Uvarov's 1937 statement was based directly on experimental facts, but his 1947 one appeared in an essay without the supporting data, it will be as well to give them here.

Desert Locust hoppers cease marching at midday on hot days and come to rest in the coolest available situations (Fraenkel 1929; Predtechensky 1935*b*; Kennedy 1945). Marching starts, on the other hand, at 26° C according to Volkonsky (1942), or even 22° C according

to Kennedy (1939), temperatures which are far from 'excessive' for these insects. It is equally clear that adult migration does not require an 'unfavourable' temperature. Bodenheimer (1929) put the limits for 'normal activity' of mature, *ph. gregaria Schistocerca* adults in the laboratory at 20 and 42° C. In his more precise study Hussein (1937) separated a 'normal activity' range between 23 and 36° C from a range of increasing 'nervousness' between 36 and 46° C. The first flights by individual swarm members appear in the morning at body temperatures within and below Hussein's range of 'normal activity', as Gunn *et al.* (1948, pp. 16 and 39) have shown. The taking-off observed at that time is by numerous, separate individuals scattered throughout the swarm (p. 169), and it is most unlikely that the temperature threshold for it is much lowered by mutual stimulation. Stimulation of one individual by others soon takes a hand, but is not a primary or a necessary condition for repeated taking-off.

Mass flight cannot be regarded as spontaneous in the sense that isolated flights are, owing to the occurrence of mutual stimulation, and observations of isolated *gregaria* locusts *starting* on migration have not yet been recorded. Hence it is at present impossible to say at what temperature migration would start without the aid of mutual stimulation. Possibly the required temperature would be higher than for swarm migration. But the fact remains that Volkonsky (1939) found that the threshold body temperature for mass taking-off by locusts in a large cage varied between 31 and 37° C, and Gunn *et al.* (1948) found that the *highest* body temperatures recorded at stream-away in the field varied between 27 and 41° C on different occasions. That is to say the start of mass migration often occurs when the locusts' body temperatures are well within Hussein's range for normal activity. Waloff's (1946) finding that the flight activity of Desert Locust swarms in East Africa remained at a high level as long as the average *maximum* temperature was above 20 to 22° C (cp. Predtechensky, 1935) was strikingly paralleled by the finding of Gunn *et al.* that mass departure occurred at air temperatures between 17 and 23° C.

Mass migration is not caused, therefore, by excessive temperatures. On the contrary, Volkonsky (1939) found that his caged swarm ceased taking-off when body temperatures reached 45° C. This contrasts sharply with Hussein's laboratory observations, in which 45° C was the temperature at which 'nervousness' passed into 'excitement'. In the field, Olsuf'ev (1930) found a swarm of *Locusta migratoria migratoria* settled at midday at a screen temperature of 35° C and remarked on the difficulty of making the locusts fly; they migrated only when the temperature was below 30° C. Similarly, Predtechensky (1935*b*) found that young swarms of *Schistocerca* in Turkestan rested in shady positions during the daytime when the air temperature reached 35° C, and did not take off until it fell again to 30° C in the evening; and Bodenheimer (1944) records a midday lull separating morning and afternoon periods of migratory activity by *Dociostaurus maroccanus*. Telenga (1930) did observe a *Schistocerca* swarm taking off at midday at a temperature which must be regarded as excessive. These locusts were resting on the ground, apparently owing to the very hot weather, for most of the morning, and were driven finally to take off only when the air temperature reached 40 to 42° C, so that this seems to be an exceptional case. During the present observations adult migrants were not seen resting on the ground at high temperatures, and fledglings were observed migrating, although interruptedly, throughout days when the maximum screen temperature reached 40° C. But older locusts were seen, during the heat

of the day on such very hot days, to accumulate at a high and presumably cooler air level where they merely circled about, so that they had effectively ceased migration even without settling.

The immobilizing effect of high temperature probably explains why swarms have been reported to fly at night instead of by day in hot weather. Night flying is of course difficult to observe, and is probably more common than the literature suggests. Regnier (1931) reported that swarms migrated at night in Morocco when the air temperature was over 27° C. Captain A. Lea (unpublished observations kindly supplied by the Anti-Locust Research Centre), working in Tripolitania in June–July 1944, and finding the young swarms of *Schistocerca* disappearing from the coastal districts and reappearing farther south, although they were seldom seen in flight during the day, concluded that most of the migration was occurring during the hot nights. Observers in Algeria (1929) come to a similar conclusion during the southward migration of 1929. And Rao (1942) writes: ‘In the summer months it is probable that migration takes place in the evening or early part of the night, while in the autumn months and in winter the nights are cold and movements probably occur during mid-day or early afternoon.’ The context is not quite clear, but Rao appears to be referring here to both phases, solitary and gregarious.

The contradiction between these field observations, showing maximum flight activity at moderate temperatures, and the laboratory results of Bodenheimer (1929), Parker (1930) and Hussein (1937) showing maximum activity at excessive temperatures, is merely apparent. We now know that the old idea of a simple, direct relationship between temperature and activity is entirely misleading.

From the laboratory side it has been shown that activity is a complex phenomenon, and cannot be measured physiologically, say by the oxygen consumption or rate of locomotion of such animals as are found moving at any chosen moment (Nicholson on *Lucilia cuprina*, 1934; Gunn & Hopf on *Ptinus tectus*, 1942; Fraenkel & Gunn 1940). If we measure the amount of activity, e.g. by the ratio of moving to resting animals, rather than the rate of locomotion, we find the shape of the temperature-activity curve varies according to the rate of change of temperature. When the temperature changes very slowly, or, what amounts to the same thing, when insects are exposed for long periods to a series of constant temperatures, the maximum activity occurs at an *intermediate* temperature, nearer to that of cold stupor than of heat stupor, which it seems legitimate to call the *optimum* temperature for the insect from a behavioural point of view. When the temperature is rising slowly in the laboratory, activity at a lower temperature than this optimum surpasses the level reached after a long stay at the optimum. With further rise of temperature, activity falls below the level found after a long stay at the optimum. Activity rises again only after a considerable further rise in temperature, but now steeply, to the ‘frenzy’ just preceding heat stupor. The different curves seem to reflect the varying interference by nervous reactions to temperature changes, against the background of the direct ‘metabolic’ or ‘releasing’ effect of temperature.

Laboratory studies on temperature and locust activity could not have revealed any similar effects because the activity was not measured quantitatively. Bodenheimer (1929), Parker (1930) and Hussein (1937) graded activity on an arbitrary scale without taking note of the proportion of individuals in motion at any given moment. From their accounts one might

think there was a simple, direct relation between activity and temperature. That seems to be the origin of the idea that mass migration, which is activity of a very intense kind, must be caused by excessive temperatures. This idea derived some support from the behaviour of locusts in temperature gradients. There they collect at moderate, intermediate temperatures and do so partly because they come to rest, that is, are less active there. But behaviour in a temperature gradient, too, depends on its steepness, that is on the rate of change of temperature to which the insects are subjected as they move along the gradient. Activity levels at various temperatures in a given gradient have no universal application. While information on the temperature-activity relations of locusts remains incomplete, it has at any rate been shown that very rapid temperature changes have not a direct, but an inverse ortho-kinetic effect; a fall of temperature provokes movement and a rise stops it, over the range of moderate temperatures (Kennedy 1939). Some further information is available concerning another kind of activity, feeding, in *Schistocerca gregaria*. Husain, Mathur & Roonwal (1949) found that the amount of food consumed per day was at a maximum between 33 and 37° C, falling off at lower and higher temperatures, the maximum rate of development being at about the same intermediate temperature.

If maximum activity were to occur at excessive temperatures, as a fixed law, that would imply that activity itself was something 'abnormal', imposed on the animal directly from outside, and that complete inactivity was the normal state. In fact, complete inactivity is abnormal behaviour for locusts. In the field the maximum *sustained* activity occurs at moderate temperatures, as it might also, judging from the work on other insects, under appropriately arranged laboratory conditions.

Inasmuch as they show maximum activity at moderate, and minimum activity at excessive temperatures, migrants in the field behave in a way that corresponds with the behaviour of non-migrants. Thus Volkonsky (1942) coined the expressive term 'euthermy', defined as the external conditions (the range of available temperatures) permitting non-migrant locusts to maintain their body temperature at the preferred level. He showed that in such conditions individual *congregans* hoppers of *Schistocerca gregaria* wandered freely within the habitat, which they did not do at lower or higher temperatures. The amount of undisturbed activity among various non-migrant *solitaria* or *congregans* populations of the same species observed by the writer (1939), appeared to decrease after the insects had come down to the ground in the morning, increased again as the morning basking period progressed, and then decreased still further when 'basking-places' became so hot that the insects retired to the shade. On cloudy, winter days when the screen maximum did not reach 30° C the period of basking and wandering freely continued right through the day. On cloudless, spring days when the maximum exceeded 30° C such activity gave way to almost complete inactivity during the hot midday hours—except for occasional individuals which emerged on to open ground and became at once violently active until they regained the shade. Similarly, the activity of a number of species of non-swarming Acrididae on a sand-dune in Palestine (Bodenheimer 1935) decreased steadily after reaching a maximum when the soil surface temperature was about 35° C. In consequence, diurnal activity showed a single, midday maximum in spring and autumn, but two maxima separated by a midday lull in summer. This fact is familiar to collectors, and was justly emphasized by Rao (1942) in connexion with the estimation of locust populations in the field.

The difference between migrant and non-migrant locusts, therefore, is not that migrants are provoked into mass movement by excessive temperatures which non-migrants somehow escape. Both are most active over a period (that is 'spontaneously' active, apart from immediate reactions to more or less sudden temperature changes) at temperatures that are optimal, not unfavourable for them. Migrants and non-migrants differ rather in the intensity of their normal activity at moderate temperatures. And if migratory flying is the normal activity of *gregaria* locusts when at or near their preferred temperature, which is the temperature to which their various temperature reactions tend to return them, then those reactions will also conspire to keep the insects flying 'automatically', as Shumakov (1940) suggested with regard to the marching of hoppers. Since Gunn *et al.* (1948) recorded body temperatures ranging up to 41° C at the time of mass stream-away, it may well be that migrating locusts often have body temperatures within the range where activity has ceased to be 'normal' and has become slightly 'nervous', for nervousness begins at about 36° C on Hussein's scale. On this scale, in fact, gregarious locusts are somewhat nervous even at the temperature preferred by them, 40 to 42° C, and if they tend to keep to that temperature not only in the laboratory but also, as seems probable, in flight, then migrants must be habitually somewhat nervous. In this sense, Hussein may have been quite correct in saying that adults in full flight are not behaving normally. That is a very different thing from saying that migration is abnormal in the sense of being caused by temperatures that are excessive, i.e. well above the preferred temperature. If migrants spend most of their time in a state of slight 'nervousness' that is due to their own exertions, released by temperatures below those causing nervousness. When they reach Hussein's 'excitement' temperature, migration tends to stop. If the slight nervousness of migrating locusts is to be classed as an abnormal condition, then it can only be said that it is normal for *gregaria* locusts to behave abnormally. It is the insects themselves that are 'abnormal', which is simply another way of saying that migrants are insects with a peculiar physiological constitution.

These conclusions accord with Uvarov's (1928) original views to which he has since returned, but the theory that migration is provoked rather than released by temperature has recently been revived by Gunn *et al.* (1945):

'Locusts will not fly if the body temperature is too low. It appears that mass departure is not due, however, to a *metabolic* effect of the body temperature, once that is high enough, but is a *reaction* to air temperature.'

The other possibility, that the air temperature might act 'permissively' in bringing about mass departure, was discussed in Gunn *et al.* later paper (1948), but considered on the whole less likely than their original suggestion:

'Apart from the effect of radiation, the factors affecting the difference between body temperature and air temperature will depend directly or indirectly on the energy of flight. It is conceivable that the interrelations between them will be such as to result, once a steady state is reached, in a relatively constant excess of body temperature over air temperature, and that the fundamental constancy at stream-away is the body temperature of locusts which have been flying for long enough to reach this steady state. The complexity of the interrelations makes this somewhat improbable. Alternatively it may be that the relative isolation of superficial parts like the antennae...will bring them close to air tempera-

ture... A reaction to air temperature through receptors on such appendages would then be consistent with the field observations' (1948, p. 38).

Let us examine the argument here, for the question is of fundamental importance. If the hypothesis of a nervous reaction to temperature causing mass departure were well founded, it would lead to the rather unexpected conclusion that the overriding behavioural characteristic of gregarious locusts, persistent migration, was not an outcome of their general physiological make-up, but was due, in essence, to one special reflex peculiar to them. The question may be considered in two parts: first, why mass stream-away should be considered a reaction to *air temperature*; and secondly, why it should be considered a nervous reaction at all.

The reasons for emphasizing air temperature as against body temperature were:

'The most consistent data were for air temperature; this was... 17–23° C (average, 20° C) at the beginning of stream-away...'

'Careful consideration of body temperature data reveals no consistent relation between them and stream-away, except that body temperature was always above the permissive temperature for flight (20° C.) at stream-away. The warmest locusts caught ranged from 27 to 41° C at that time on different days' (1948, pp. 5, 6).

The suggested explanation of stream-away in terms of a nervous reaction to temperature (1948, p. 38, and quoted above) came as the conclusion of a discussion opened thus:

'This fact, that stream-away is comparatively independent of the body temperatures which we recorded is unexpected and requires explanation' (1948, p. 30).

However, on the previous page the method of recording body temperatures was described in detail, and this is referred to in the summary on p. 6:

'Since stream-away occurs as a result of sustained flight, as distinct from the short flights commonly seen earlier in the day, and since representative body temperatures from locusts in sustained flight could not be obtained, it remains possible that there is a relation between body temperature in flight and stream-away.'

Since the recorded body temperatures were not those of locusts that had been flying long enough to have reached thermal equilibrium with the air, it is not after all unexpected that they varied much more widely than did the air temperatures recorded at the time of mass departure. These data do not seem to provide any evidence against the body temperature being the deciding quantity for stream-away.

As to whether mass departure is a reaction at all Gunn *et al.* (1948) point out (p. 31) that 'locusts do not simply take-off when a certain body temperature has been reached'; and they go on to say (p. 33):

'This conclusion suggests that the assumption of upward flight, as a preliminary to stream-away, is a behaviour reaction, the stimulus for which can hardly be body temperature, because of the great range of maximum body temperatures when it occurs.'

Taking-off may, indeed, occur only in response to some trigger stimulus and probably does so in response to many kinds of stimuli. But such triggering-off occurs repeatedly *before* mass departure; it is not what is new at that time.

‘Using an old terminology, the short flights made by many locusts before stream-away would be called *trial* flights, which are repeated as long as the conditions for take-off are adequate, until more continuous flying occurs as soon as the conditions in mid-air are appropriate for staying up’ (p. 38).

When one is considering taking-off, which is a dramatic change in *individual* behaviour, it is natural to think in terms of reactions, but the mass departure depends, as far as the individual is concerned, on the mere continuation, in place of the previously repeated cessation, of an activity, flight, which was already in train, and which is destined sometimes to continue for many hours. This does not suggest a reaction at all.

The idea of a reaction would not have arisen, it appears, were it not for the fact that mass departure starts, as a rule, rather suddenly, as the only obvious break in the morning sequence of movement-patterns. The main object of Gunn *et al.* was not to make a causal analysis of the process by which a swarm becomes finally launched on migration, but rather to find what governed the timing of this process. They considered the density of the locusts as likely to govern the intensity of gregarious excitation, and in that sense as a factor comparable with other regulating factors which vary from time to time and place to place, like temperature humidity, wind, etc. And among these, the factorial analysis pointed to air temperature as the most important influence setting the time when flying about passed over into stream-away.

So far the argument is straightforward, but at this point it makes a leap, with the suggestion that the air temperature may not merely determine the *time* of mass departure, but be its direct cause, through a nervous reaction. This is a different proposition altogether, not supported by the observations and at variance with the authors’ statement (p. 30) that ‘stream-away is essentially a mass phenomenon’. It is also at variance with their suggestion (p. 24) that ‘the unity both of flight activity and of orientation observed at stream-away might be due to mutual stimulation’. If these statements are correct, then the main reason for postulating a nervous reaction as the cause of mass departure is removed. Unity of flight and of orientation are themselves the direct cause of mass departure, as discussed elsewhere (pp. 230–232).

The suddenness of mass departure appears to come from a sudden change in the movement-pattern within the mass, which occurs automatically when mutual stimulation between individuals reaches a certain intensity. Such a change, dramatic though it often is, requires only a small quantitative increase in the same ‘permissive’ action that temperature had been exerting before the mass departure. It does not require a new type of temperature effect, a nervous reaction, to come suddenly into play.

The persistent flying observed among gregarious Desert Locusts, we may conclude, is a characteristic of the insects themselves, as near to being truly spontaneous as any so-called spontaneous behaviour. Temperature may be one among a number of stimuli which provoke *taking-off*, but its most important role in mass migration seems to be that of a releaser, permitting locusts that have taken off to stay warm enough to fly on.

Height of flight. Waloff (1946*b*) and Rainey & Waloff (1948) have produced some direct and more circumstantial evidence that Desert Locusts reach considerable heights with the aid of thermal up-currents. On this assumption and in the light of an analysis of the meteorological data, they were able to work out, with an impressive degree of plausibility,

how certain long-range swarm movements over the sea could have been brought about. Swarms are sometimes seen pillaring upwards rather like cumulus clouds, in a way that suggests the locusts are in fact at the mercy of strong thermal convection. Such convection requires strong solar radiation to heat the ground, and it would seem to follow that locusts would be found flying higher, on the average, in sunny than in cloudy weather, and so higher in the hot dry seasons than in the rainy seasons.

The evidence of such an effect of temperature on the height of flight is so far fragmentary. Regnier (1931) observed swarms of *Schistocerca gregaria* rising vertically during the warmest part of the day, an act which enabled them to cross the Atlas Mountains. Bruzzone (1936), who claims to have kept a single swarm of *S. cancellata* Serville (= *paranensis* Burmeister) under continuous observation during a whole month, stated that the greater strength of the sun the higher rose the swarm. A similar impression was formed during the present studies.

It was decidedly warmer and sunnier during the Iranian observations than during the Kenya ones. In Iran locusts were seen flying at more than 30 m. on fourteen occasions (43%) and at more than 100 m. on six of the total of thirty-one occasions quoted in table 2. In Kenya they were seen flying at more than 30 m. on only four occasions (25%), and at more than 100 m. on two out of the total of sixteen occasions quoted in table 2. There were four other occasions when locusts were seen very high (more than 100 m.): two in Arabia (table 2, nos. 1 and 3), and two when the swarm in question had been engaged in mating and egg-laying, in Iran on 1 June 1943 and in Kenya on 22 April 1944. There were, therefore, twelve occasions altogether when locusts were seen flying very high, and on all but one of these it was remarked that the weather was unusually hot. The exception was on 27 June 1944 (table 2, no. 49) when the swarm reached 200 m. as early as 09.00 hr., but this was the swarm which had been repeatedly activated by low-flying aircraft.

On eight of the other eleven occasions the high-fliers were not moving in a common direction but milling about, and on six out of these eight occasions the very high-fliers occurred as scattered individuals and were either separated by a considerable gap from locusts at lower levels (nos. 20 and 21 in table 2; and mating swarms on 1 June 1943 and 22 April 1944), or occurred in the complete absence of lower locusts (nos. 15 and 30 in table 2). The high-fliers in these six cases were only just visible to the naked eye when the sun caught their wings. They appeared and disappeared between the observer and the sun in a way that indicated they must have been present, if invisible, over a large expanse of sky. They extended upwards as far as could be seen even through glasses. These six cases of very high circling flight all occurred when it was extremely hot and thermal up-currents were frequent, often in the form of violent 'dust-devils'.

Since the height at which the insects fly can make a great difference to the direction and speed of their movement over the ground, it is an urgent matter to obtain more data on the effects of temperature, and especially of radiation and convection, on the height of flight. But it should be borne in mind that when locusts rise in hot weather, this may not be merely because they are lifted passively by the rising air. Rising might be to some extent a reaction to temperature, one of the locusts' means of regulating their body temperature and keeping it near the preferred level (cp. p. 241). Even when the mechanical lift is mainly due to the rising air rather than to active climbing flight, the locust's act of permitting the air to lift

it in this way cannot be regarded as an entirely passive matter; the locust might, for example, settle, if too hot, rather than remain air-borne.

Direction of flight. Several authors have attributed changes of direction by flying swarms to supposed changes of air temperature. Thus, Regnier (1931) observed a swarm of *S. gregaria* arriving at Rabat (Morocco) with a hot wind from the south-east. Upon reaching the sea-shore, it turned and flew along the coast. All swarms observed during several months turned along the coast-line in this way. He suggested that the change of direction was induced by the encounter with the supposedly cool air over the ocean. Bruzzone (1936) describes a swarm of *S. cancellata* Serville encountering a cool southerly wind and turning on itself with a period of much confusion during which the locusts in front were turning and meeting others still coming up before meeting the cool air. Later, the same swarm, flying northwards, encountered currents of cool air descending from some hills, turned west, and passed through a gap between the hills. Both changes of direction Bruzzone attributes to the drop in air temperature. Predtechensky (1935*a*) made similar observations in Iran in 1929–30, for he concluded (in somewhat confusing terms): ‘meeting with cold air media, locusts endeavour to escape their influence, by directing their flights toward a warmer stratum of air’ (Mr Koffler’s translation, 1938, p. 70). There are also various reports, quoted on pp. 202–203, of swarms changing direction on encountering, and flying with, the wind in front of storms.

In most of these cases it is possible that a sudden change of air temperature contributed to the observed change of direction, but nothing more definite can be said for other changes in conditions, such as the speed and structure of the wind, occurred at the same time. It is fairly safe to assume that horizontal air-temperature gradients are too irregular or too gentle to permit the *continued* kind of directed temperature reaction implied by Predtechensky in the quotation above. Even on the ground, where steep gradients do exist among vegetation, directed temperature reactions did not appear to play much part in the behaviour of locusts (Kennedy 1939). The changes of direction at the sea-shore reported by Regnier (1931) and on p. 198 could have been visual responses to the changed ground pattern (see p. 208), and it seems very doubtful whether any but the lowest-flying locusts would feel a change of temperature at the moment of meeting the shore-line in an off-shore wind.

On the whole, evidence of a direct influence of temperature on the direction of flight is inconsiderable and unconvincing.

The sun as a directing influence

There is no evidence that the direction of swarm flight bears a consistent relation to the direction of the sun and no one has suggested this. De Lépiney (1928) is the only observer who has been convinced that flying swarms were oriented by the sun, for he observed numerous cases of courses being toward it, although tracks were not necessarily toward it, being deflected by the wind. But even he said that such orientation occurred only sometimes.

It would be unwise, however, to neglect the possibility that migrants do orient to the sun, merely because their observed orientation to it is variable or because other influences, notably wind, seem to have a more important orienting action. Thanks to the work of Grassé (1922, 1923), Fraenkel (1929, 1930), Volkonsky (1939) and others a number of orientation reactions to both radiant heat and light have been established in locusts in the labora-

tory. Only further work can decide to what extent these reactions occur during migratory flying, but it is improbable that they do not occur at all.

De Lépiney drew a parallel between his observations of swarms flying toward the sun and his own and Grassé's laboratory experiments showing positive phototaxis and thermotaxis. As far as the heat reaction is concerned, the parallel may not be valid because, in the laboratory, the radiant heat source was close to the insects which were therefore moving in a gradient of radiant heat intensity and perhaps of air temperature also, and may have been directing themselves along these gradients. With the heat source as remote as the sun, however, no such gradients exist, so that if the fliers were indeed reacting to the sun's radiant heat, the reaction was not necessarily equivalent to the positive thermotaxis seen in the laboratory. Phototaxis, on the other hand, could occur to the sun as to an artificial light in the laboratory.

It happens that the orientation reactions of locusts to radiant heat and light have been worked out more fully for resting ('basking') locusts than for walking or flying ones. These reactions involve perpendicular orientation to both heat and light rays when the locusts are below, and parallel orientation to the rays when they are above, their preferred temperature, about 40° C (Volkonsky 1939). These reactions form a part of the locust's system of regulating its body temperature—a function presumably as necessary in flight as on the ground.

Two different methods of body-temperature regulation are known in locusts: changing the orientation to heat rays, and moving to a cooler situation. Flying locusts must often be in danger of overstepping their preferred temperature (see p. 236), and may be more dependent on changing their body orientation as a means of temperature regulation than are locusts on the ground. The other method of temperature regulation would be less effective in flight than on the ground, because cooler situations are less immediately to hand in the air. If the locusts de Lépiney observed flying toward the sun were reacting to it as basking locusts do, their parallel orientation to its rays would indicate that they would have been above their preferred temperature in any other orientation. Their flight toward the sun would therefore be in no way comparable with the movement toward the heated plate in the laboratory, for there, when the locusts became too hot, they walked away from, not toward the plate.

It has been suggested that the direction in which hoppers start marching may be perpendicular or parallel to the sun's rays according to their basking orientation at the time (Kennedy 1945). Since the wind is often very weak in the morning and appears to have an important orienting influence on adults when it strengthens later, morning might be the best time to look for the basking type of orientation to heat and light rays among the adults also. Gunn *et al.* (1940) concluded that their data gave no support to the idea of parallel orientation to the sun's rays at stream-away, but that it was possible orientation was often at right angles to the rays. That would be expected if the locusts streamed away while still below their preferred temperature, which the body-temperature measurements suggested they usually were. More data are required on orientations not only at stream-away but also before it, when changes of orientation might be particularly revealing. The four observations on the morning behaviour of migrant swarms recorded here (figure 1, p. 171) included some such data but are too few for further consideration at the present. Thus while there is so far no evidence that orientation reactions of the basking type occur in flight, they might

be worth looking for, especially when temperatures are very low or very high and wind orientation is unlikely.

Quite apart from their 'basking' orientation reactions to radiant heat and light, locusts are known to be positively phototactic up to their preferred temperature, under certain conditions (Volkonsky 1939; Kennedy 1939, pp. 491–494). The positive phototaxis is rather easily suppressed by other reactions. While resting, adults will orient perpendicularly to 'cold' light rays. But they change their orientation to one parallel with the light rays just prior to making a move, and so walk or fly *toward* the light (Kennedy 1939, p. 450). There is nothing in Volkonsky's account (1939) nor the writer's (1939), to rule out the appearance of positive phototaxis at any light intensity and any body temperature, provided there is no overriding reaction to radiant heat, wind, etc. Locusts taking off after sunset appeared to be reacting in this way when they flew predominantly toward the light western sky (p. 175) as was observed also in solitaries (Kennedy 1939, p. 450).

Otherwise, however, there is as yet no evidence that phototaxis has an important influence on the direction of migration, for there is an alternative explanation of Lépiney's examples of flight toward the sun, in terms of the basking type of parallel orientation to the heat and light rays.

While there is no satisfactory evidence that the sun has any *lasting* orienting influence on hoppers or adults, there is good evidence, as far as hoppers are concerned, that it has a temporary, direction-stabilizing influence, through the sun-compass reaction.

As seen in other insects, a light-compass reaction is one in which the insect moves at a constant angle to a light source, but an angle that is not laid down permanently (Fraenkel & Gunn 1940). It might be called a 'temporary fixation reaction'. The points on the eye at which the light is 'fixed' are not limited to one or two, depending on the body temperature, as in the true light-fixation reaction described by Volkonsky (1939) as part of the locust basking-reaction complex. Instead, any point at which the light has been held for some time becomes the fixation-point at which the insect itself then holds the light by means of compensatory turning movements made in response to any subsequent shift in the position of the image. Such a reaction, in respect of the sun, has been demonstrated in marching hoppers (Kennedy 1945).

Direct evidence of the same kind is still awaited for flying adults. Although it did prove possible to make temporarily shaded fliers reverse their direction by throwing the sun's reflexion on to them from the side opposite to that on which the real sun had been shining, only five individuals were so treated, and they emerged too quickly from the shade (p. 196). But, unless we are to postulate an innate sense of direction beyond the reach of experimental investigation, we are obliged to find an external cause for the notable degree of stability of orientation observed among migrants when temporarily deflected by the wind or by moving or stationary obstacles (pp. 196 and 197). However important compensatory reactions to wind may be, locusts do not follow every little shift in the wind direction even when their tracks are deflected, and they quickly revert to their previous course after temporary changes of course due to sporadic wind gusts or to obstacles, even when isolated from other locusts. The sun, acting through a compass reaction, is at present the only external cause that seems not only possible but probable in such cases. Once again, more observations and experiments are called for, especially when the sun is obscured.

Assuming as a working hypothesis that the sun-compass reaction does occur in adults, the direction-stabilizing capacity of this reaction is obvious. It could make a primary directing influence like the wind even more effective than it otherwise would be in preserving the uni-directional character of migratory flight, for full weight would thereby be given to the mean wind direction while the disruptive effect of temporary wind shifts was reduced to a minimum. When locusts then encounter a temporary cross-wind, the tendency to turn into the new up-wind orientation is resisted, just as diversionary attempts by man are resisted, and a temporary compromise seems to be reached between an up-wind orientation and the old, previously established one. This is illustrated in figure 8 and is also described, although otherwise interpreted, by Williams (1933, 1942).

Again, if a locust had 'fixed' the sun's position in its eye while close to the ground, and then rose, it would be able to continue in the same up-wind orientation when too high to react to apparent ground movement. There is commonly much internal circulation in flying swarms, upper and lower fliers changing places from time to time. Orientations could be then corrected with respect to the wind during approaches to the ground and retained during excursions to higher levels.

When the wind is negligible near the ground, or in any wind at heights where apparent ground movement is too slow to provoke orientation responses, the light-compass reaction to the sun could become of first importance. It and 'gregarious inertia' (p. 194) could then serve as continuously acting, *complementary* orienting influences, as has been described for marching hoppers (Kennedy 1945). But it is emphasized that neither of these reactions could originate an orientation with respect to the ground. They serve only to stabilize and perpetuate courses set by other means. They cannot therefore explain the geographical trends in migration.

Landscape

Field observations of hoppers (Kennedy 1945; Chauvin 1947) strongly suggest that features of the terrain over which they are migrating influence their direction above all visually. This is still more probable for adults which migrate out of mechanical contact with the ground. This section is therefore headed not 'Terrain', but 'Landscape'.

Avoidance of obstacles. Deft avoidance of obstacles is one of the characteristic features of migrant behaviour (p. 197). Migrants approaching an object in the line of flight change direction before reaching it, fly round or over it and resume their previous direction as soon as the object—tree, man, or whatever it may be—has been circumvented. We are not concerned here with the resumption of the previous direction, which is attributable to the sun-compass or some other direction-stabilizing reactions; but with the change of direction on approach to the object. Such obstacle-avoidance is the migrant's repeated, typical reaction to conspicuous objects, even stationary ones, whereas non-migrant locusts, when not actually being chased by conspicuous 'objects', are often seen to direct themselves toward and settle on them (p. 199). Such positive attraction appears among migrating locusts only when migration is ceasing, as in the evening when the whole swarm will soon be settled. It seems, therefore, that migrants in full flight are in a peculiar 'mood' or state of reactivity, which disappears as soon as steady migration flying ceases; or it might be more accurate to say that migration ceases because the 'mood' disappears. A fully com-

parable state of affairs was found in hoppers. While on the march they also circumvent or surmount obstacles and retain a constant direction by means of their sun-compass reaction and gregariousness despite temporary deviations, but as soon as marching slackens they lose their common direction and are attracted to and settle on conspicuous objects (Kennedy 1945).

The visual nature of obstacle-avoidance was especially clear in the black cloth experiments (pp. 197–198). The cloth was no real obstacle in the mechanical sense, but only a novel and striking feature, appearing suddenly in the locusts' field of view. The essence of the locusts' reaction was a change of direction away from a suddenly appearing, conspicuous, visual feature. The cloth was, of course, a very small, quickly passed feature at most. To appreciate the significance of the reaction one must consider what would happen if the novel feature were far bigger. In that case it would cut across a large part of the insect's retina, and would persist in doing so for a time despite the insect's progression. Here again it is useful to consider hoppers (Kennedy 1945) in which comparable behaviour was observed, but in convenient miniature, since their rate of locomotion and field of view on the ground are restricted. On encountering a new vista, whether a suddenly appearing large obstruction, or at the brink of water, or at a precipice, they paused, 'peered' and then, sometimes after a phase of confused pottering about, turned and moved along parallel with the brink of the visual obstacle. Adults might be expected to behave similarly in relation to physical features of suitable size, which recalls Regnier's (1931) and other observations of swarms that changed direction upon reaching the sea-shore and flew thereafter along the shore-line (pp. 198 and 240). It seems much more likely that the locusts were reacting to the sight of the sea than to a change of temperature such as Regnier suggested. Thus the evidence lends substance to Rao's (1942) suggestion that 'migratory flights are presumably halted by a sight of the great barrier of the sea'.

Locust swarms do often cross the sea despite the above evidence that they sometimes turn aside rather than leave the land. If the avoidance be visual, it is not difficult to imagine conditions under which it would not occur, for instance with locusts that were high, or where the shore-line was not conspicuous.

Once a new direction parallel with the visual obstacle's border was assumed, it was persisted in by both hoppers and adults. Hoppers moved along parallel with lateral 'walls', whether of water, earth or shrubs, following every bend (Kennedy 1945), even when the hoppers concerned were out of sight of one another so that mutual vision was ruled out as a guiding factor. They did not have their direction corrected repeatedly by physical encounters with the 'wall'. Evidently they were keeping alined with it by visual means.

Chauvin (1947) made a revealing observation in this connexion. Writing of obstacle-circumvention by marching *Dociostaurus maroccanus* hoppers, he says:

'Lorsque l'obstacle laisse une ouverture médiane de 15 centimètres au minimum, les Criquets ne cherchent plus à le contourner mais s'engouffrent en masse par l'ouverture.'

This parallels the behaviour of a *Schistocerca* swarm already described (p. 198), which turned to stream through a gap in an escarpment, thereby resuming the direction it had been following before being diverted along the escarpment a few minutes earlier. To quote Chauvin further:

‘Un obstacle allongé parallèle à la direction générale paraît sans aucun effet, même s’il porte une ouverture de 15 ou 30 centimètres de large, mais à condition que la voie soit libre de part et d’autre.’

Such failure to respond to openings in a wall paralleling the established direction of movement, so long as the way ahead lay open, was observed many times also in Desert Locust hoppers. The statement (Kennedy 1945, p. 256) that hoppers ‘continued, as they moved along, to keep at an approximately fixed distance from the walls by visual means’ was misleading in so far as it implied that the hoppers were constantly responding to visual stimulation from the side. Chauvin’s observations show that it is to gross changes in its *forward* field of view that the insect is primarily responding in such cases, by turning in the face of an obstruction but moving straight ahead as long as the way ahead lies open. Similar behaviour is said to guide young turtles down to the sea from their hatching sites on the shore (Parker 1922).

This is not *phototactic* behaviour, however, in locusts. The increase in illumination from in front experienced upon reaching the edge of a precipice, or of water, had the same arresting and deflecting effect on the hopper as had the decrease of forward illumination experienced upon coming up against a dark, upstanding obstacle. The reaction is to some gross change in the anterior field of view, not to illumination as such. Thus the responses concerned in obstacle-circumvention and, equally, those concerned in rectilinear movement along rectilinear features of the visible environment, constitute yet another type of visual compensatory reaction, in this case to changes in the anterior field of view. The reaction is another special case of the general tendency of migrating locusts to ‘keep their visible environment as constant as is compatible with their own continued movement’ (Kennedy 1945). Greater or smaller changes in the lateral field of view are an inevitable accompaniment of continued movement. They are produced by objects which are not in the direct path of the insect and so not incompatible with its continued movement. But objects in the direct path of the insect are often physically incompatible with its continued movement and, physically or merely sensorily incompatible, they do in fact provoke active compensatory responses having the effect of restoring to the anterior field of view the general character to which the moving insect has become accustomed. If this be true of hoppers, then we should expect to find adult migrants behaving with relation to a ‘wall’ on land much as do hoppers, although on a larger scale. Such behaviour is in fact well known: the tendency of swarms to move along valleys. This was observed generally in mountainous Iran apart from the particular instances given above, and has been mentioned by other authors (Predtechensky 1935*a*; Zolotarevsky 1930; Vosseler 1905). Other factors are probably involved, wind and temperature especially, but this tendency is at least consistent with the principle of ‘movement in the direction of maximum constancy of the visual field’ (Kennedy 1945). Again, more experimental work is needed on adults.

Attraction to conspicuous objects. Previous work has shown that both hoppers and adults are attracted to conspicuous objects in their vicinity (de Lépiney 1928; Predtechensky 1935*b*; Bodenheimer 1944; Kennedy 1939, 1945). This attraction seems to be similar in principle to the attraction of non-migrating *gregaria* hoppers to one another. It may be regarded as a compensatory reaction with respect to conspicuous visible movement, when that move-

ment is due to the reacting insect's own locomotion, the attracting object remaining still (cp. p. 228). According to all the authors who have described visual attraction of hoppers to inanimate objects, the attraction is not evident when locusts are migrating steadily. It is evident, in both hoppers and adults, only when they are ceasing migration or for the time being non-migrant. This distinction between the behaviour of full migrants on the one hand and slackening migrants or non-migrants on the other was confirmed during the present studies (p. 199).

The general impression that migrant swarms select for roosting the most conspicuous trees in the neighbourhood was also confirmed during the present studies (p. 199). Lépiney mentions this phenomenon, and quotes cases where it was clear the attraction could not have been other than visual (cp. Kennedy 1939, pp. 447-9).

There was little evidence that swarms in full flight were attracted in the same way to conspicuous objects. On the contrary, they avoided them as discussed in the previous section. There is a popular belief among agriculturalists that swarms do descend for choice upon green (and in desert countries often therefore conspicuous) crops, but this may be a biased view. Systematic and unbiased data on this matter would probably be difficult to collect, but one aspect of it invites experimental study; the effect of external and internal conditions on the locusts' responsiveness to the conspicuous objects they meet on migration. Speaking of hoppers, Volkonsky (1942) states:

‘Cette attraction...visuelle se manifeste de plus en plus au fur et à mesure que la végétation...se dessèche. Elle disparaît lorsque la végétation est détrempée par une pluie où lorsque l'état hygrométrique de l'atmosphère est élevé.’

Volkonsky never published the evidence for this statement, but there are some indications that the excitability of adults, and their orientation to wind, may depend on their water relations (below, p. 247), so that the possibility of their susceptibility to attraction by conspicuous objects being conditioned in the same way would be worth investigating.

Moisture

A number of authors have given consideration in recent years to moisture as an influence on locust migration. There is some fresh direct evidence of its effects and some evidence from correlative studies of routine reports, while experienced students like Rao and Strelnikov have given their strong impressions on the subject.

Volkonsky (1939) found that caged swarms of Desert Locusts engaged in spontaneous mass flying only when the mean relative humidity during the preceding 24 hr. had been 65 % or below, and except for four out of the nineteen occasions only when it had been 59 % or below. The total relative humidity range covered by Volkonsky's observations was 52 to 75 %. He discussed temperatures also, but unfortunately he does not give any detailed figures, and does not indicate to what extent his observations warranted clear conclusions regarding the separate effects of humidity.

Concerning the pre-conditioning effect of air and insect water content upon the behaviour of the insects, Volkonsky remarks in a later paper (1942) that the tendency for individual Desert Locusts released from cages to embark on sustained, uni-directional flight is favoured by desiccation. He also states (in quotation above) that the apparently visual attraction of conspicuous vegetation for gregarious hoppers is most evident when the general

vegetation is drying up, and disappears again with a fall of rain or rise in air humidity. Strelnikov (1936) found that hoppers lost half their weight in a day's march and states that water was the main material lost. He goes on to say that the loss of water first increases 'irritability' and then causes depression. Rao (1942) also stresses low humidity as an 'irritating' factor leading to the evacuation of first the winter-spring and then the summer breeding areas of *Schistocerca* in India. Again he offers no direct evidence, basing his opinion on the correlation between the onset of hot desiccating conditions and the emigration of the locusts. Partly from circumstantial evidence and partly from observations on caged locusts from swarms, Rao believes that locusts which have been subjected to drought conditions are particularly susceptible to activation by the stimuli (including moisture) brought by, or even preceding, rain or dust storms.

In the laboratory Kennedy (1937) found that *Locusta* of all stages were activated by a rise and inactivated by a fall of humidity, provided the exposure times were short. If successive dry and moist exposure periods lasted many hours no difference in activity was apparent. Locusts starved for some days in a low humidity, continued to show a preference for dry air when offered a choice, partly through the kinetic reaction just mentioned. Key (1936), on the other hand, found that older *Locusta* hoppers reared very wet were activated by exposure to a dry atmosphere, while those reared very dry were activated by exposure to a wet atmosphere.

The results of these laboratory experiments are confused and incomplete, but further support for Volkonsky's, Strelnikov's and Rao's views comes from an observation by Tauber, Drake & Decker (1945). They found that *Melanoplus bivittatus* fed on fresh, moist plants were quiet and not easily excited, whereas when fed on desiccated plants the insects were 'hyper-irritable', jumping and flying about at the slightest disturbance.

The most striking illustration of both humidity responses and humidity-conditioning of other responses comes from the field observations of Bodenheimer (1944) on *Dociostaurus maroccanus*. To some extent these observations were anticipated by those of Shotwell (1930) on *Melanoplus mexicanus*. Observing that *Dociostaurus* adults seemed to be attracted from a distance to his experimental pans of moistened bait, Bodenheimer tried pouring a small quantity of water on the ground when numerous locusts were sitting about nearby. At once locusts from up to 20 or more metres away, and in a narrow cone of directions down-wind of the moistened sand, took off, flew low toward and came down at it. From other directions only insects immediately adjacent to the water came to it; farther away they remained quite immobile. The responses were most marked during the heat of the day, and the attracted insects 'drank' avidly from the wet sand grains. Afterwards they flew off, now across-wind.

The same results were obtained in repeated trials. On one occasion members of a swarm already in flight, across-wind, were observed, as soon as they arrived down-wind of moistened sand, to turn up-wind and fly in a definite stream across the main swarm direction, to the moisture. The experiments established the existence in *Dociostaurus* of:

(i) *a conditional, direct, hygro-kinesis*: locusts resting in relatively hot, dry conditions were strongly stimulated into flight by an access of moist air; whereas in other conditions they were less affected;

(ii) *humidity-conditioning of wind orientation reactions*: moisture in the wind not only stimu-

lated sensitized locusts into flight, but also enhanced or evoked the (probably optical) reactions leading to up-wind orientation, which ceased when the locusts had drunk adequately.

It is not clear whether the effect on wind reactions was direct, in the insect, or indirect, a result of making the insects descend to where such reactions would become stronger anyway, on the optomotor theory (figure 13, p. 213). The second suggestion is the simpler of the two behaviourally, but there are precedents, among insects, for the first suggestion of wind-borne substances evoking wind orientation (Flügge 1934; Tinbergen 1935; Kalmus 1942).

Bodenheimer's observations were confined to small, local movements, but point (i) could be important for long-range movements also, and supports Rao's suggestion above (p. 247). The only case in which the idea of humidity-conditioned wind orientation has been put forward on the basis of a large body of data concerns the movements of *Chortoicetes terminifera* in Australia, analyzed by Key (1942, pp. 31–34, 61–62 and 75–77). Correlating the predominant monthly flight direction in each locality with wind directions and humidity gradients, in 1937–8, he found that swarms flew 'more or less' up-wind in 49 % of cases but 'more or less' up the humidity gradient in 74 % of cases; there were 661 cases in all. 'More or less' here means anything up to 45° to left or right of the due direction. Thus the locusts flew up the humidity gradient but with or across the wind in 25 % of the cases. A similar marked predominance of up-humidity-gradient flights were found in 1936–7 and in 1938–9.

How much meaning these consolidated average figures have is very doubtful, for they tell us nothing about the actual wind and humidity conditions experienced by any swarm. No conclusions can be drawn from the data about the reactions of *Chortoicetes* until direct observations under known conditions are available. But it is important meanwhile to consider Key's suggestions in this connexion in the light of Bodenheimer's work and the optomotor theory of the behaviour of wind. This subject has engaged the attention of other writers on insect migration (Williams 1949; Waloff 1946). We cannot yet answer the questions at issue, but the lines of future work will depend very largely on what is now considered more and what less likely to be the correct solution.

Key's (1942, p. 76) argument was as follows:

'the simplest assumption would be that swarms orient their flight according to the direction of the wind, but discriminate between "moist" winds and "dry" winds, flying with the latter and against the former. Owing to the marked tendency for moving air masses to retain the properties they possessed at their source of origin, down-gradient winds at any station are always moister than the mean relative humidity for the station, while up-gradient winds are always drier than the mean, and these departures may be considerable.'

From what has been said here about wind orientation, and from Bodenheimer's work, it appears that Key may be proved right, as far as orientation against moist winds is concerned. Given appropriately conditioned locusts, up-humidity gradient flights might be due to moist winds encouraging first taking-off and then up-wind orientation, whereas dry winds might discourage taking-off and be less likely to impose active up-wind orientation when flight does occur. A moist wind might be able to induce up-wind orientation better than

a dry wind for the further reason that the moist wind keeps the fliers low while the dry one does not, although Bodenheimer's evidence of this was not so good. But there is no evidence to support Key's suggestion that dry winds produce down-wind orientation directly, that is simply by reversing the insects' reaction to moist wind.

Williams (1949) has suggested that the humidity changes experienced by insects in the course of their local movements through the micro-climatic 'patchwork' and in the diurnal humidity cycle, are greater than those they would experience through changes in the wind direction. The local changes would mask those due to wind changes so that the latter could have no clear influence on flight orientation. The whole matter requires investigation, but this argument may not be as conclusive as it at first appears. The laboratory experiments described and Bodenheimer's field observations, however explained, suggest that it is the *change* of ambient air humidity which is the effective stimulus for taking-off and enhanced orientation to wind. The diurnal humidity cycle involves slow changes, and other factors like temperature and light confine the flights of locusts to a limited part of the diurnal humidity cycle. More rapid changes will be experienced in moving through the micro-climatic 'patchwork', but it is also possible that the insects respond, not to humidity changes as such, but to them only when combined with wind.

Key (1942, p. 76) himself points out that 'flight up the humidity gradient might result from a differential response to winds differing in other qualities than moisture content, for example temperature or strength'. There is reason to suppose the directing influence of wind (not *responses* to it) may be reversed by such other factors (see part II), but the possibility that humidity can similarly condition the wind's directing influence on some locusts, cannot be excluded.

The effect of insect desiccation and wind moisture on wind orientation is not, however, conspicuous in the Desert Locust. These conditions are by no means indispensable for up-wind orientation to dominate a whole migration trend, as witness the up-wind migration of the Desert Locust in early spring (p. 203) when there is plenty of fresh green food available and the rains may still be on.

Rain has often been described as having at least a temporarily hindering effect on flight and sometimes a spectacular one (Cheesman, 1929; Gunn *et al.* 1948, p. 52; Harrison, 1929; U.S.A. 1878, 1880), but the effect of the accompanying drop in air temperature cannot be separated in the field from the effects of rain itself. On the whole it appears that rain itself provides surprisingly little hindrance to migration, as appeared during the present observations (p. 178). From her analysis of records of swarms found flying and settled at different seasons and in different districts in East Africa, Waloff (1946*a*) concluded that most of the reduction of flight activity occurring during rainy seasons was due to reproductive behaviour.

Migration as a special type of behaviour

Only some of the aspects of the behaviour of migrant, adult, gregarious phase Desert Locusts have been discussed here, and deficiencies in our knowledge have been pointed out many times. But we have now a sufficiently full picture of their behaviour, provided it is taken together with that of migrant hoppers, to deduce what essentially distinguishes migratory from other kinds of behaviour.

Activity

The most unmistakable feature of the behaviour of *gregaria* locusts is their extraordinarily persistent locomotory activity. Over a wide range of external conditions, swarms take to flight in the morning and fly on, or alight only to take off again repeatedly, until evening. And they do this day after day, once recovered from the last moult, and with some reduction during mating and egg-laying, until death. The hopper bands behave in much the same way.

This 'irrepressible' locomotory activity naturally requires suitable environmental conditions, but these are conditions that can only be regarded as moderate and favourable for the species (pp. 232–236). Conditions that are excessive or unfavourable to the species, such as extremes of heat and cold, strong wind, etc., restrict rather than enforce marching and flight. External conditions thereby determine during which hours of the day or night, migration occurs in a given region and season (pp. 233–234), but they do not 'force' it to occur. Even the external influence of other band or swarm members is not essential for the *gregaria* individual to show its extraordinary activity (p. 194). That influence seems to be an important means of reinforcing activity in bands and swarms (pp. 224–225) but even so cannot be regarded as an extraneous force. The *gregaria* individual is so constituted as to expose itself preferentially to its fellows' influence and is peculiarly sensitive to it. We might regard as forced the development of the migratory habit during the change from the *solitaria* to the *gregaria* phase, since exceptional circumstances are required to bring this change about. Once gregarization is complete and we are dealing with locusts of the gregarious phase, however, sustained locomotion does not depend on circumstances that are exceptional in any way.

If the behaviour of the solitary phase, or of most animals for that matter, be taken as a standard, then gregarious locusts are clearly abnormal in embarking on a course of sustained locomotion when conditions are in no way extreme. But the fact is that such behaviour is normal for gregarious locusts (p. 226). Under favourable conditions the solitary (or non-migrating *gregaria*) locust makes only intermittent movement through the day, periods of movement falling between longer periods of feeding, basking, mating, etc. Under the same conditions, the migrant keeps up extraordinarily persistent movement, 'sedentary' types of behaviour, such as feeding and basking, becoming restricted in consequence to early morning and evening. This migratory activity is characteristic of the insects themselves:

'Flying with them (gregarious locusts) may be regarded as a normal state and rest is enforced by environmental conditions' (Uvarov 1947).

Persistent locomotory activity is not in itself what distinguishes the migrant, however. Such activity is the normal behaviour of insects which are obviously not migrant, like whirligig beetles (Gyrinidae) or the many kinds of insects which form persistent swarms during the nuptial flight, such as mayflies (Ephemeroptera). What separates the behaviour of these insects from that of a migrant is not only the fact that they remain in roughly the same place, but also that their simple locomotion is readily interrupted by other kinds of behaviour: feeding and mating, respectively, in the examples mentioned. Indeed, the immediate effect of their locomotory activity is to expose them more effectively to the

specific stimuli which interrupt it: the whirligig beetle to floating food particles and the mayfly to its potential mates. Their locomotory activity may be regarded as an essential part of the activities of feeding and mating. The situation is reversed for the migrating locust. Its behaviour is dominated by locomotory activity for hours at a time, day after day, to the virtual exclusion of all else. Whatever ultimate effect this may have on the biology of the species it certainly has no immediate connexion with biological functions like feeding and reproduction.

If this most characteristic feature of migrant behaviour is to be put into a phrase, it may be said that the *gregaria* locust is subject to a powerful 'locomotory drive'. The term 'locomotory drive' is used here descriptively and objectively, implying neither consciousness nor directiveness. It means simply that the insect is in a neuro-physiological state of a peculiar kind, such that its whole behaviour is subordinated to locomotion and other forms of activity are largely shut off.

Direction

The observed tendency to keep a straight course. The second characteristic feature of the locust migrant's behaviour is its tendency to move steadily in one direction. This tendency requires careful definition, as the centre of much controversy. Williams (1949, p. 73), speaking of butterflies, has described the situation in this way:

'During a migratory flight the path of each butterfly—which would normally have been here and there, backwards and forwards, leaving the insect at the end of the day more or less where it started—is straightened out so that the insect flies steadily in one direction.'

Now it appears that steady flight in one direction occurs more often among butterflies than among locusts (Part II). And the tendency to fly straight may be less strong even in butterflies than Williams suggests, for it is difficult to see how he could be sure that one "compass" direction can be kept up hour by hour and day by day by a single insect' (1949, p. 73). At any rate, there is no evidence that locusts ever fly as straight as that and numerous cases are on record of direction changes under immediate observation by both hopper bands and adult swarms. When single swarms have been followed day after day, the line joining successive night-roosting sites has proved to be a zigzag, not a straight line (Gunn *et al.* 1948). And Waloff's (1946, p. 48, table I) analysis of the collected routine reports of Desert Locust swarms in eastern Kenya showed that the proportion of *all* swarms found in flight was almost always higher than the proportion of *flying* swarms found moving toward any one of the eight main sectors of the compass. Flight itself, not flight in one direction, is the main characteristic of migrants.

We are not here concerned, however, with the pattern of movements among whole populations of swarms, nor with the resultant direction of long-range movements the route of which can only be inferred; such matters form a separate study (Part II). We are concerned here with the movements of individual migrants, bands or swarms as directly observed and therefore over short distances and on or near the ground.

Among these, the direction of movement shows a fixity which, although very far from absolute, is striking by comparison with the more erratic movements of non-migrant locusts or other insects. When the adult gregarious locust engages in the peculiarly persistent movement characteristic of the migrant, instead of merely making periodic short flights

between intervals of feeding, basking, etc., the direction during the longer flight varies much less than do the directions of the series of short flights, for a given total distance travelled. To say that the flight path becomes 'straightened out' is no mere figure of speech, for this straightening out can be watched as an actual process, within the larger process by which a swarm becomes launched on migration in the morning. It is this straightening-out process, added to the increasing duration of flights, which actually brings about the final mass departure itself (p. 232).

The tendency of migrants to go straight, by comparison with non-migrants, is brought out particularly clearly in relation to individual, conspicuous objects, like trees, in their vicinity. The short flights of swarm members after migration has ceased in the evening, or of non-migrant fledglings, or of non-migrants in phases other than *gregaria*, are often *toward* such objects (p. 245), and individuals are sometimes seen to turn toward them when they had been moving in another direction (Kennedy 1939, pp. 430, 448; 1945, p. 257). Migrating locusts, on the other hand, are not attracted by such incidental features of their route. They are not deflected by them unless one lies straight ahead in their established line of movement: in that case the migrant does change its direction temporarily but resumes the old direction as soon as the obstacle had been circumvented.

The theory of a special directional sense. Observers have been profoundly impressed by the sight of migrants holding a straight course apparently without reference to their surroundings. This is no doubt largely responsible for the idea of conscious self-direction being introduced into discussions of migration by a number of writers of which Williams (1930) is the best-known among entomologists:

'The migrating animal is in some way conscious of, and helps to determine, the direction of movement' (Williams 1930, p. 9).

Accordingly, Williams put forward the idea of an 'innate sense of direction' as a basis for further work. Since then, he has called instead for perseverance in the search for an external guiding force, but at the same time does not seem to have abandoned altogether the original idea of an innate sense of direction.

Thus in 1942 (p. 226) he wrote: 'One would expect some external guiding force or stimulus to be concerned', and discussed the evidence, leaving the question open. At the same time he posed the complementary question: 'What evidence is there that insects are conscious of and allow for the influence of the wind direction?' This question, too, was left open, and first place in the whole discussion was given to one particular observation on *Danaus plexippus* L., which 'appears at present quite inexplicable on any theory'; and later (p. 231) cases were quoted of insects 'flying at an angle to the wind as if to allow for its influence'.

In his most recent discussion of the subject Williams (1949) said there was no real mystery about migrant orientations, only ignorance as to their causes, which he expected would be discovered, eventually, in external, physical forces. But he also said (p. 74):

'On reaching an obstacle most migratory butterflies pass *over* it rather than *round* it, when this is possible. This definite sense of orientation is often one of the most striking features of a flight.'

and (p. 75):

‘Migrating butterflies have also at times been observed to follow the windings of deep valleys, of roads through forests, and of shorelines, but these cases are small in number compared with the number of observations of definite directional sense.’

These statements are hardly compatible with the view that all orientations have external causes. If they have, then the insects always have a definite sense of orientation. At one time they may be reacting to obvious but varying external directing agencies, and so moving on a meandering course. At another time they may be reacting to as yet unknown but evidently more constant external agencies, and so moving on a straight course. The direction itself is more ‘definite’, that is, constant, in the second case of undeviating movement. But the insect’s ‘sense’, that is, its sensory dependence on external orienting agencies, is as real in the first case as in the second. Something more than orientation to external agencies must surely be meant by the term ‘directional sense’ when, the less obvious the external agency determining a given course, the more definite is the directional sense inferred. This kind of directional sense seems meaningless except in relation to a postulated distant goal, so that conscious self-direction seems to be clearly implied.

Theories of conscious self-direction invoke subjective forces as if they could take the place of the objective ones that seem to be lacking. But subjective forces can never take the place of objective ones. Conscious man himself is powerless to direct his movements without reference to external features.

There is no choice, therefore, but to examine more closely the possibilities of orientation by means of external features; and, in fact, a number of directed reactions to external features are known in locust hoppers, or adults, or both. Williams (1930, 1949) has set aside every reaction to external stimuli—except one—that has been suggested, or even demonstrated to be concerned in the orientation of flying insects, on the grounds that none of these external stimuli is constant enough to keep a migrant on a straight course over long distances. The exception was the earth’s magnetic field, the possible orienting action of which was investigated experimentally on locust hoppers by Cockbill (1942). The results were negative, as the investigators rather expected. It seems premature to set the known reactions aside in this way for two reasons. We have no evidence that migrants do hold a straight course over long distances; and long-range movements can never be explained except on the basis of the insects’ behaviour of which the known reactions form a significant part, even if these reactions can never *directly* explain the long-range movements.

Known orientation reactions. Taking the evidence for adult locusts presented in this paper and that for hoppers reviewed elsewhere (Kennedy 1945), at least four kinds of orientation reactions have been demonstrated: to fellow individuals, to the wind, to the sun and to the ‘landscape’. Gregarious re-alignment is established for both hoppers and adults, although the detailed responses involved, presumably optomotor, have yet to be worked out. Some responses to wind, such as settling or turning away from an up-wind course when backward drift begins, are better established than others, but the available information fits reasonably well an optomotor theory and an elaborated optomotor hypothesis of behaviour in wind based on laboratory work on mosquitoes. The sun-compass reaction has been demonstrated in hoppers, but not yet properly tested in adults; a similar situation exists with regard to the

reaction to shifts of the retinal images of gross features of the landscape in the forward field of view. Other directing agencies have been suggested but not demonstrated, such as orientation reactions of the basking type, to radiant heat, which may be of some importance, particularly when migration starts.

These are all reactions to gross environmental stimuli, obvious to man. Reactions to stimuli less obvious to man, such as aerodynamic changes (p. 207), although perhaps mainly concerned in maintaining the insects' immediate stability in flight, should also be mentioned. They will help, if in a minor capacity, to promote straightforward flight.

These reactions are not peculiar to the behaviour of migrants. The mutual compensation reactions of gregarious locusts occur also when they are not migrating. Wind orientation, the light-compass reaction and movement toward the 'open', have not yet been demonstrated independently in non-migrant locusts, but have been demonstrated in other non-migrant animals (Fraenkel & Gunn 1940). There is no reason to suppose any of the reactions of migrating locusts are, as reactions, peculiar to their behaviour while migrating. The migrant differs from the non-migrant, therefore, in the changed *pattern* of its reactions rather than in any novelty about the reactions themselves.

The problem, then, is not to discover 'the methods by which migrating insects . . . keep to a fixed direction over long distances and over long periods of time' (Williams 1942, p. 226). Nor is it, primarily, to discover some new kind of reaction. The problem is to discover how the several known reactions of the migrant to external features become *organized* into a particular pattern: a pattern which includes many changes of direction, but also a good deal of steady flying in one direction.

The organization of orientation reactions into the pattern peculiar to migrants. The point of departure in considering this problem is that similar reactions to the same external stimuli can produce, either direction changes, or straightforward movement, according to the circumstances. Changes of direction and straightforward movement have been set against one another in the past (see the quotations from Williams 1949, pp. 74–75, given on p. 252–3), as evidence of two distinct principles of orientation; temporary reactions to merely disruptive external features, and the special directional sense. If we dispense with the second principle, then field observations of changes of direction provide the natural experiments needed to elucidate the causes of unchanging direction. The next task, therefore, is to compare the circumstances under which these two types of movement appear.

Changes of wind speed or direction, when the wind is strong and the insects are flying low, provoke various reactions including changes of orientation. In a more moderate wind of fairly steady direction, on the other hand, low-fliers fly steadily on in one direction, say against the wind. According to the optomotor theory, they are kept on that course partly because any turn produces gross transverse image-movement which is compensated by a turn back into the up-wind orientation. Thus the insect itself, if it does not fly straight when there is a steady wind, produces gross changes in the apparent movement of its visible background. These changes brought about by the insect itself in a steady wind are comparable with the changes experienced by a steady insect subjected to a changing wind. In compensating the resultant image-movement, the insect minimizes the changes, and so flies straight ahead when the wind is steady but deviates when the wind changes.

When two columns of migrating hoppers or adults meet at an angle, compensatory

responses of insect to insect cause mass changes of direction, or 'gregarious re-alignment', as when two bands or swarms cross, or when the wind induces 'gregarious reversal'. In a single advancing band or swarm, not subject to the mass impact of insects moving in another direction, similar responses help to maintain steady movement in one direction (p. 228).

A striking new feature in the landscape such as a tree or a glittering body of water lying across the path of migrant hoppers or adults, may cause them to change direction before actually reaching it. But if such conspicuous features are elongated, like a shore-line or an avenue through vegetation, the movement of the migrants may be canalized along a path parallel with the line, straight or meandering, of the external features, the only path on which gross transverse image-movements can be avoided (p. 245).

The sun-compass reaction is the one reaction to gross external features which is observed to cause only steady movement in one direction for considerable periods, and not changes of direction, under natural conditions. Presumably the reason for this is that the sun's own direction, unlike that of the other features mentioned, does not change rapidly. But if its apparent position be changed rapidly with a mirror, it does produce changes of direction, very strikingly (Kennedy 1945). In nature, it seems, it is only the insect's own deviations from a straight course which cause sufficiently rapid changes of the sun's position in the insect's eye to bring the sun-compass reaction into play, which reaction therefore serves to keep the insect on a straight course.

Thus the evidence suggests a very simple conclusion: the circumstances in which a change of direction occurs are those in which a gross change occurs in one or more of the external features to which the migrants show orientation reactions; while the circumstances in which movement is straightforward are those in which no such gross external changes occur. Thus changes of direction, and fixity of direction, contrasted though they seem, stem from one and the same tendency on the part of the migrants. That is the tendency to avoid, or rather minimize, changes in their sensory relations with the environment. If these relations are sufficiently changed by a change in the environment, the migrants are caused to change their direction accordingly. If the environment remains constant, then the migrants keep their own direction constant, for otherwise, if they deviate, their sensory relations with environmental features are changed as much as in the former case when those features themselves changed.

The tendency to go straight as an outcome of the locomotory 'drive'. In reacting to changes in the sensed environment in such a way as to minimize those changes, i.e. in a *regulatory* manner, migrants behave as non-migrants do. Such sensory regulation is one of the most fundamental functions of behaviour in general and is no more peculiar to migrants than are the kinds of reaction by which the regulation is effected.

At the same time, behaviour does not consist merely in maintaining as constant an environment as possible. Behaviour consists of various positive activities by which the animal lives and reproduces itself, and it is these activities which are facilitated and guided, to some extent, by sensory regulation. In the course of such an activity the animal undergoes major changes in its sensory relations with the environment, changes which it does not minimize by regulatory reactions, but which on the contrary it accepts and reacts to in ways that further change its external relations. We may therefore make a working distinc-

tion between reactions having the immediate sensory-regulating effect of minimizing changes in the animal's environmental relations, and the function of smoothing the animal's path in the carrying out of a number of vital activities, on the one hand, and, on the other hand, reactions having the immediate effect of changing the animal's environmental relations, and the function of contributing directly to the carrying out of some specific vital activity, such as feeding or mating. No teleological assumptions are involved here, even if, with the 'objectivistic' behaviour school (Tinbergen 1942), we designate the tendency to behave in a certain complex of ways associated with a given vital function, as a 'mood' or 'drive' named after the function (but see p. 258).

The behaviour of the migrant is dominated by a locomotory 'drive', as we have seen. Neither the kinds of orientation reaction, nor their joint, sensory-regulating function, are peculiar to the migrant, but the locomotory drive is. In the migrant, locomotion becomes elevated to the status of a 'vital activity'. It is in the locomotory drive, therefore, that we must look for the origin of the tendency to go straight, since that also is peculiar to the migrant. For analytical purposes we may distinguish, quite artificially, two ways in which the locomotory drive transforms the pattern of regulatory reactions into one which results in straightforward movement.

Consider first the external circumstances of the insect. Compare the circumstances of a non-migrant locust, such as one of phase *solitaria*, or *gregaria* but non-migrant because engaged in reproductive activity, with those of a migrant *gregaria* locust. Owing to the variety of activities on which the non-migrant spends its time—feeding, basking, moulting, mating, avoiding enemies, etc.—it carries out only a limited amount of locomotion, and that intermittently. It spends its time on the ground or vegetation where a great variety of conditions are found within a small compass. It responds to the stimuli provided by many individual details of the habitat. Each plant, for example, plays its individual part in evoking diverse responses, as a source of food, as shelter from wind, as shade from the sun, mechanically as a resting place, and as an attractant, conspicuous object. Micro-climatically, the environment is a 'patch-work'. Temperature, for example, varies abruptly from point to point, and the insect's thermokinetic responses seem to play a dominant part in its whole diurnal behaviour pattern. The locusts' responses to such stimuli are seldom directed, and when they are, the directions taken are inconsistent. While a shrub, for example, may serve as a directing (attractant) stimulus for a while, the insect soon reaches it and the shrub then resolves itself into a variety of other stimuli: mechanical, thermal, gustatory, etc.

The non-migrant's regulatory reactions help to keep it within its particular habitat, and therefore within a more limited range of conditions than it would experience without them. But its movements within the habitat are in many directions and cannot possibly be in only one, when it is merely 'pottering about', responding to many incidental details of its environment in the course of a variety of 'sedentary' activities.

Contrast with this the behaviour of the migrant. For the migrant there is only one drive and one activity, not 'sedentary', but locomotory. Impelled by its overriding locomotory drive, the adult spends its time in the relatively uniform environment of the air, out of reach of the kaleidoscopic micro-changes it would suffer on the ground. The migrant hopper, too, keeps to the most open, uniform terrain accessible to it. The four types of reaction suggested above as important in adult migratory behaviour are all *visual*. Compared with changes in

the flying insect's field of view, other external changes, as of temperature and humidity, are slow and infrequent. And while the non-migrant reacts visually to the individual shrubs about it as isolated objects, they become for the migrant merely units in a moving procession, and it is to this movement and not to the separate units composing it that the migrant reacts, on the optomotor theory, in orienting to the wind. A single object must be large, striking and in the immediate line of flight before it can evoke a separate response from the migrant.

Because the migrant is constantly moving on, it necessarily experiences continuous change at least in its visible environment, unless it is flying very high or in the dark. It accepts these continuous small changes as a concomitant of its own movement, as a moving but non-migrant does in a more limited way, without reacting to each passing detail. Because of the special environment it creates for itself, the migrant does not encounter sudden discontinuous changes as often, in a given distance travelled, as the moving non-migrant; but when the migrant does experience such changes in the environmental procession past it, it does respond, by regulatory reactions. The discontinuities may be due either to the 'looming up' of outstanding new features as it moves along, or to a change in its relation to old, in themselves relatively unchanging, features like the sun, the wind or fellow-locusts, a change caused by its own deviation from a straight path. As a result of regulatory responses to changes of this second type, the insect's deviations are minimized and the tendency to go straight emerges. Thus the tendency to go straight is to some extent an indirect outcome of the locomotory drive, that is, an outcome of the peculiar external circumstances the migrant experiences. The tendency is seen also in non-migrants, but is not so conspicuous there, partly because non-migrants do not travel so far in one movement, and do not remain in so uniform an environment.

However, persistent locomotion does not necessarily create a tendency to go straight, even if it does so in gregarious locusts. In some insects, such as the Gyrinid beetles and mayflies already cited (p. 250), persistent locomotion is accompanied by frequent direction changes. Despite their disorderly superficial appearance it is precisely through these frequent direction changes that continuously moving but non-migrant insects maintain an orderly, regulated relationship with their surroundings; either with some one conspicuous feature, as in midges (Gibson, 1945) or mosquitoes (Bates, 1949), or with several features in combination, as in Gyrinids (Brown & Hatch, 1929). The environmental relations of continuously moving insects may thus be stabilized in one of two types of orientation: (i) by keeping a straight course through compensatory responses to those gross external features which remain with the insect, so to say, as it moves, while 'ignoring' incidental, local features; or (ii) by constantly changing direction through compensatory responses to fixed local features. The latter appears to be a higher form of orientation, allied to what Tinbergen (1942) has called 'pharotaxis'.

The difference between these two types of orientation evidently reflects a difference in the reactivity of the insects to similar stimuli, and in the pattern on which their reactions are organized internally. Associated with those differences, the biological functions of the two types of orientation are also different. The locomotion of non-migrants forms part of their immediate feeding or mating activities, while that of the locust migrant does not, having an uncertain biological effect which is discussed elsewhere (Kennedy, in preparation).

Moreover, if migrants travel farther, without being distracted by incidental features along their route, than do non-migrants, it is their locomotory drive which not only impels the migrants but which also prevents them reacting to the incidental features. This is evident from the fact that when migration is slackening, but before the locomotion itself has ceased, the migrants change their reaction to conspicuous external objects, from avoidance of them to attraction to them (pp. 199 and 245). We must picture the steady locomotion as the clearest expression of a generalized 'drive' or 'mood' (Tinbergen 1942) which expresses itself also in the detailed reactions of the insect—or, as we might say, in the insect's changed 'attitude' to the same external features. That is not to say that the change of 'attitude' is determined wholly physiologically, by internal causes, and still less that it implies a conscious state. It is probably the combination of the peculiar neuro-physiological state of the *gregaria* migrant, plus the peculiar pattern of its sensory experiences during continuous locomotion, which together bring about the change of 'attitude' during actual migration.

In the whole complex of the *gregaria* locusts' migratory behaviour we have an example of instinctive behaviour in the broad sense of Lorenz's recently proposed usage: that is (Tinbergen 1942; Thorpe 1948), behaviour comprising two main components. There is a stereotyped automatism, either walking, hopping or flight, which is the instinctive action in the strict sense (*Erbkoordination* of Lorenz), and there is an elaborate, non-stereotyped 'coating' of reactions to specific stimuli (the '*Taxis*' component of Lorenz) which guide the automatism in operation.

'The "*Erbkoordination*" can as a rule be released by a combination of external and internal factors. Usually, the internal factors evoke a preparedness to react to certain external stimuli in a certain way, in other words, the external stimuli are more specific than the internal causes' (Tinbergen 1942).

Thus, the locomotory automatism appears in locust migration, as we have seen, mainly from internal causes of a general ('metabolic') nature, although it probably has to be released by trigger stimuli. But, in addition, the same internal causes create in the migrant a special type of reactivity to certain external stimuli, the ones which the migrant experiences repeatedly as a result of its own activity.

It is necessary, however, to bear in mind that we are dealing here only with behavioural events and not with physiological or psychological ones. The observed behavioural events, such as persistent locomotion, or a particular pattern of regulatory reactions, are the effects of as yet largely unknown physiological causes to which the locomotory *drive* and sensory-stabilizing *tendency* are ultimately referable. While it may be convenient to label such behavioural tendencies according to their specific effects or functions, this does not mean there is a comparable specificity in their physiological causes. A merely quantitative physiological change, as in the concentration of a hormone or in the pattern of central nervous excitation, can produce a completely new pattern of behaviour. Lorenz's concept of *reaction specific energy* seems unfortunate because it implies a specific one-to-one relationship between internal cause and external effect. If we visualize a given behaviour pattern as caused by some equally specific, counterpart material, 'energy' or process in the nervous system, then it is all too easy to translate this directly into subjective terms. If the behaviour pattern be conceived as existing in some potential, already-differentiated form in the

animal before it appears in overt acts, then cause and effect become reversed, and we have something very like a pre-existing idea or purpose postulated as the cause of the overt act.

When speaking of the locust's locomotory drive, therefore, we mean a behavioural tendency having definite physiological causes which have yet to be discovered, and not a tendency attributable to a subjective urge or 'appetite' for locomotion (cp. *preference*, p. 212). At the same time, while we are dealing with behaviour we can recognize the locomotory drive, and the sensory-stabilizing tendency, as tangible and important entities, the effects of which can be examined although we do not yet know their physiological basis.

Locomotion is a relatively simple activity from a behavioural, if not from a physiological, point of view. It does not involve the elaborate sequences of different reactions to specific stimuli, such as are involved in the other kinds of instinctive activity that have been cited in this discussion: feeding and mating. During the latter activities, these specific reactions prevent the animal from stabilizing its environmental relations to any striking degree, although immediately regulatory reactions are also occurring frequently and serving to minimize external changes which would otherwise disrupt the given specific activity. The behaviour of the migrant, however, is made up, apart from its locomotion, almost entirely of reactions of the immediately regulatory type. This is, no doubt, one reason why migratory behaviour has often seemed to be something quite apart from all other kinds of behaviour. The migrant's tendency to go straight is the sensory-regulating type of behaviour maintained in so exceptionally pure a form that it has given the impression of veritable independence of the environment, instead of the delicately adjusted, direct dependence which it in fact expresses.

The tendency to go straight, and the going itself, are both outcomes of the locomotory drive. That drive, the only feature peculiar to or 'innate' in migrants, is not itself directional in any sense. There is no '*directional* urge' in the migrant, no 'innate sense of direction'. Locomotory activity—'going'—is more persistent and unconditional than going straight. It is the direct outcome of the causes subsumed under the term locomotory drive. In that sense locomotory activity is the primary aspect of migratory behaviour, while going straight is a secondary one. Going straight is more conditional, an outcome not only of the special locomotory drive but equally also of the general function of sensory regulation. Going straight is simply a means of solving an old biological problem in a new context: the problem of environmental stabilization in the context of persistent locomotion.

Locomotory 'drive' versus sensory regulation: the key to migratory behaviour. The external changes to which an animal makes regulatory responses are commonly changes to which it exposes itself, in the course of its activity under the influence of one or other type of 'drive'. Nowhere is this seen more clearly than in the behaviour of migrants. Migrants 'keep their environment as constant as is compatible with their own continued movement' (Kennedy 1945). In this connexion orientation reactions have received a disproportionate amount of attention, for they are by no means the only ones employed by migrants in regulating the changes they bring upon themselves. They vary their height of flight, and even the amount of their locomotory activity itself, as part of their regulatory reactions. Sensory regulation of many kinds is constantly brought into operation by the insect's locomotory activity.

The migrating insect's two inseparable tendencies, the tendency to *travel* with consequent exposure to sensory changes, and the tendency to *minimize* those *changes*, are best illustrated

from the behaviour of adult locusts in wind. The wind is very liable to sudden changes, and since it bears the locusts, it is the most disruptive influence with which they have to deal. The locust's regulatory reactions to the stimuli provided by the wind tend, if they seldom entirely manage, to keep the locust's displacement over the ground under its own control, that is, to keep its ground speed close to its air speed and its track close to its course. On the optomotor theory, that is a consequence of the locust having a certain preferred retinal velocity and air speed. The reactions evoked when the wind causes departures from these preferred values have the effect of minimizing the wind's tendency to deviate tracks from courses and indefinitely to raise ground speeds. High ground speeds, due to down-wind flight, are compatible with maintenance of the preferred retinal velocity and air speed, at moderate height. But in practice, the increase of wind speed with height favours lower, up-wind flights (p. 223), and the variability of wind speeds militates against the perpetuation of a given course higher up where intermittent settling is not a ready means of sensory regulation. The locust can keep control, in the objective, resultant sense indicated, without regulating its behaviour according to the wind so long as the wind speed is well below the locust's own air speed. But when the wind is stronger, the locust's regulatory reactions come into play and help it to keep control, but cannot completely succeed because the wind is so erratic a force.

Thus, were the regulatory tendency clearly shown by the locust's reactions to be taken, hypothetically, to its logical conclusion, so as to give the insect complete control over its ground speed and course, it would fly only when the wind was negligibly weak. But its locomotory drive will not allow that, and it does fly in wind. The regulatory tendency shows itself in the insect's settling repeatedly, if near the ground, whenever the wind begins to carry it backwards. Again, were the evident regulatory tendency taken to its logical conclusion, the locust would always fly near enough to the ground to be able to see its wind-created, apparent movement and minimize it, by orienting against the wind and settling when no headway could be made. But its locomotory drive, its tendency to climb in certain circumstances and the thermal up-currents to which it exposes itself, prevent it from staying within quick-settling range of the ground, or even within visually responsive range of it. If it sees it is being carried away but cannot quickly settle, it turns down-wind where at least it is going the same way as it is facing, the only form of control left to it. And its own activity often leads directly or indirectly to its losing even that amount of control.

The locust migrant is engaged, in effect, in a constant struggle against the sensory disruption engendered by its own irrepressible locomotion. The key to its whole behaviour is the opposition between two powerful tendencies combined in the same insect: the tendency to locomotion and the tendency to sensory regulation.

PART II. A THEORY OF LONG-RANGE MIGRATIONS

SUMMARY

Cartographical analysis of the seasonal and geographical patterns of Desert Locust migration points unmistakably to wind as a key element in the determination of long-range migrations. Cartographical and behavioural analyses show that the consistency of direction responsible for long-range trends is not created in the same way as the striking stability and unanimity of direction immediately observable during flights over short distances, which was considered in Part I. Long-range movements are resultant trends, emerging from a mesh of more or less confused movements. Behaviour analysis indicated that there was a constant struggle between the locusts and the wind for control over the locusts' displacement over the ground. Displacement through the forward flight exertions of the locusts and displacement through being carried by the wind are both common and can continue for long periods. It is obvious that wind-dominated displacement could create a long-range trend, and the behaviour observations indicated that locust-dominated displacement too could create a trend, but again, only under the influence of the wind. The following theory of long-range migration is, therefore, put forward.

The creation of geographically directional trends. Displacement due to the locusts' own exertions can develop into a geographical trend if the locusts persistently resist carriage on the wind and make headway against it, actively orienting into it at least intermittently. Displacement due to wind carriage can develop into a trend if the locusts persistently fly, yet signally fail to resist carriage on the wind and go with it. There seems to be no other basis of long-range trend-creation. Locust-controlled and wind-controlled displacement thus tend to be in opposite directions, up- and down-wind respectively. An actual geographical trend appears among the swarms in a given region and season when one of the two kinds of displacement predominates decisively over the other.

External and internal factors can help or hinder the locusts' resistance to wind carriage. An important means by which external factors do this is by influencing the height at which the locusts fly, for the higher they fly the less they can resist wind carriage. These helping and hindering factors act in a valve-like manner and are therefore called 'rectifiers'. They do not cause displacement, nor direct it, but they do determine how fast and in which out of various possible directions a trend will actually occur. They determine whether the locusts or the wind shall mainly effect the locusts' displacement and so determine whether the over-all displacement shall be up-wind, down-wind or negligible. The outstanding rectifiers seem to be temperature, locust age and the wind itself. Steady and moderate winds, moderate temperatures and the vigour of fully hardened locusts favour up-wind displacement. Gustly and stronger winds, high temperatures, active convection and the weakness of young locusts favour down-wind displacement. Geographical trends tend to, but do not always parallel the *prevailing* wind direction, for the most frequent wind may not be the one having the strongest rectifying qualities.

Organization of trends into a pattern. The pattern of trends reflects the swaying fortunes of locusts and wind as rival agents of locust displacement. The pattern of rectifiers moulds the pattern of trends. When a new generation of swarms is appearing at the start of a new dry season, the high temperature and weakness of the locusts conspire to minimize the locusts' control over their own displacement, rectify their displacement down-wind and produce a spectacular geographical shift of the whole population of swarms. Such seasons alternate with seasons of more confused swarm movements, in which lower temperatures and the fully developed powers of the locusts combine to put them on a more equal footing in the struggle with the wind. Control passes now to the locusts, when up-wind trends may appear; and now to the wind, when down-wind trends appear. Often, the two are so evenly matched as agents of displacement that there is no predominant trend one way or another. The cartographical confusion among swarm movements in the in-between seasons is due partly to the transition from one prevailing wind direction to another. Geographical redistribution of the swarm population is due in these seasons, more than in the others, to regional temperature differences acting, to use an analogy, ortho- and klinokinetically. In other words, swarms disperse in and from warmer regions where they fly more, and more straightforwardly, and become trapped in cooler (often mountainous) regions where they fly less and change direction more.

Make-up of the whole pattern. Multiplication and mortality are essential elements in the whole pattern of migrations. They determine where swarms will be available to start on migrations, and where migrations must end for lack of migrants. The environmental patterns (rainfall and temperature especially) mould the migration pattern, therefore, not only behaviourally and mechanically, but also in these 'biological' ways. Some trends are regularly 'abortive' in the sense that they do not lead to new breeding grounds, while other trends are regularly 'successful' in that they do lead to new breeding grounds. Many successful and spectacular long-range movements are made when the insects have *least* control over their own displacement. The whole pattern involves the cyclical repetition of both abortive and successful trends.

When tested in a preliminary way against known examples of long-range migrations, this theory shows promise, but its validity cannot be properly gauged until much more information of a suitable type has been amassed.

Other ideas of insect migration are discussed in relation to the present theory, such as that long-range directional movements cannot be explained in objective terms and imply the existence of an innate sense of direction; that such movements are essentially passive; that no explanatory hypothesis can be expected until the complicated interaction of the many factors involved has been unravelled; and that migrants are guided by some one physical agency yet to be discovered. It is emphasized that, in essence, long-range migration trends are not behavioural but rather ecological events.

INTRODUCTION

The previous part attempted a causal analysis of Desert Locust migration considered as a type of behaviour. The present one attempts a causal analysis of the geographical pattern of migrations, and, in particular, of the more spectacular long-range movements which form a part of that pattern. It is usual to treat these two problems as one, rather than separate them as is done here. But, for reasons that will be given, we cannot assume that the direction of migration over short distances, as observed directly, is determined in the same way as the direction of migration over long distances, as inferred from maps on which reports from all sources are plotted. In studying migration patterns we have to deal, not with the behaviour of a sample of migrants in the particular circumstances under which close observation has been possible, but with the net geographical displacements of whole populations of locusts: a problem of a different order. The present analysis starts, therefore, from the evidence on migration patterns derived from synoptic studies of routine swarm reports. The relevant behavioural information is then drawn upon for the construction of a new theory of the causes of long-range migration trends.

THE EVIDENCE FROM CARTOGRAPHICAL ANALYSIS

The large-scale patterns of locusts' migrations are probably better known than those of any other insects. There are fewer scientifically interested field observers of locusts than of, say, butterflies, but there is an army of economically interested locust observers whose reports have been collected for years. The first detailed study of such reports concerning the Desert Locust was Predtechensky's (1935*a*), on migrations in Persia and adjacent countries. The pre-requisites for more fully documented studies had already been provided in 1929, when the Anti-Locust Research Centre was established in London, and in 1930, when the International Locust Conference at Rome agreed that reporting arrangements be improved and all reports sent to that Centre for collation. The accumulated material was first presented in the form of annual summaries of movements and breeding (Uvarov 1933*a*, 1933*b*, 1934, 1935; Uvarov & Milnthorpe 1937*a*, 1937*b*, 1939). Since then, the seasonal patterns of breeding

and migration of the Desert Locust in single regions have been analyzed and published (Rao 1942, for India; Waloff 1946*a*, for eastern Africa; Donnelly 1947, for West Africa). The subject has passed entirely beyond the stage of ingenious inference from fragmentary data, which was all that was possible when Bodenheimer (1932) made his bold, speculative sketch of the cycle of Desert Locust swarm movements. Information services are still imperfect and interpretation of the information sometimes difficult, but it is now possible to draw conclusions on a firm foundation of facts, and even to give countries advance warning of locust incursions.

The migration patterns that have emerged from all this work are not yet complete and present a complex and fluid appearance. Reducing the movements to a system of distinct trends is not easy. No two years show quite the same pattern, and yet several years must be taken into account in delineating trends with sufficient assurance. These points are stressed because insect migrations are often thought to be more regular than they are. The trends finally revealed in this way are real, nevertheless.

Knowing the migration patterns, the next task is to establish their relation with the patterns of weather and geography. With that aim in view, a great deal of statistical work has been done on the Australian Plague Locust (*Chortoicetes terminifera* Walk) (Davidson 1936; Key 1938, 1942, 1943). The value of undertaking the heavy task of such detailed correlations in ignorance of likely causal connexions seems rather doubtful, and Predtechensky (1935), Rao (1942) and Waloff (1946*a*) have confined themselves to drawing more general conclusions concerning the influence of the environment upon the Desert Locust's migrations. Waloff's work in particular led to conclusions directly relevant to our problem of the behavioural basis of long-range migrations by the Desert Locust.

Her general conclusions were as follows:

The pattern of breeding areas and migrations is complex and inconstant. Major trends represent merely predominant, not universal behaviour among the swarms concerned. However,

'The seasonal trends of migrations and the changing location of breeding areas combine to produce a fairly regular pattern of seasonal distributions over East Africa. This regularity depends on the physiological responses of the locust to climatic factors, whose pattern changes from season to season in a regular manner, and is not due to migration or breeding cycles inherent in the species.'

It is clear from Waloff's work that although the locusts fly with extraordinary persistency, their movements do not suggest any search for suitable breeding areas, or for food (cf. Uvarov 1928, 1944). Their movements are too disorderly to suggest a set tendency to fly in a particular direction. They have no 'goal'. Although the directions they take must therefore depend on external factors there is no one such factor with which locust movements are consistently related. The direction of migration must be determined by a complex of causes and not by any single type of reaction or single external factor.

The positive findings of Waloff's study were as follows:

(1) Flight activity persists as long as the average monthly maximum temperature exceeds 20–22° C (cp. Predtechensky 1935), a conclusion borne out by independent evidence on the air temperature at the time of departure of swarms in the morning (Gunn *et al.* 1948).

- (2) Swarms rapidly evacuate areas where the weather is hot and dry.
- (3) Flight activity is reduced during egg-laying periods in rainy seasons, but not noticeably by rain as such.
- (4) The main effect of physical relief appears to be in reality an effect of temperature on activity—swarms become trapped in the highlands in the cool season, and are then released and spread out from there when temperatures rise.
- (5) 'Apart from some important exceptions when swarms migrate across or against the wind, the major trends of migrations are down the prevailing winds, and change with them.'
- (6) 'The distribution of swarms at any season is thus largely dependent on the pattern of air temperatures and winds.'

We are not directly concerned with *breeding* when trying to interpret migration patterns in behavioural terms. Breeding areas represent temporary halting-places for sexually-mature swarms and the points of origin of immature ones. In this way they form an essential element in the seasonal pattern. What principally determines their location is fairly clear. 'The incidence of breeding depends, among other factors, on the incidence of suitable rainfall conditions. Because of this and of the mobility of swarms, the location of breeding areas is not constant, but follows seasonal changes in rainfall distribution' (Waloff 1946*a*).

Nor need another essential element in the seasonal pattern, variations in flight *activity*, detain us, except for its part in determining direction (below). Flight activity, dependent primarily on temperature, is restricted until 'fledging' is complete and is temporarily reduced during mating and egg-laying. Other environmental factors, such as moisture in the air or the vegetation, atmospheric pressure and rain, do not seem to have an important effect on the amount of flying done by Desert Locust swarms, whatever may be their effects on other aspects of swarm behaviour, on other phases or other species.

Our main problem is not breeding nor activity, but the *direction* of trends, the third essential element in pattern determination. The results of cartographical studies point unmistakably to *wind* as the key factor underlying the direction of major movements. In the first place, if we reject, as a mere label on our ignorance, the idea of a long-range directional 'sense' or 'instinct' within the insect, we must look for a long-range external agency. We are not looking for an external agency which could make all swarms fly in the same direction during any season. The records show very clearly that swarms do not move in that way. We are looking for an external agency which can make enough of the swarms move in the same direction enough of the time to produce an overall trend of migration. Wind is an external agency which seems able to fill this role. More inflexible agencies, say the earth's magnetic field (Cockbill 1942) or its rotation (Chauvin 1947), the influence of which is purely hypothetical, can be neglected until the lack of any other explanation forces us to consider them. The relation between winds and migration trends is too close to be coincidental. There are significant exceptions, but the great seasonal trends are mainly with or against the prevailing wind, usually with it.

THE BEHAVIOURAL BASIS FOR THE CREATION OF LONG-RANGE MIGRATION TRENDS

In full accord with the cartographical evidence, the direction of migrants as observed directly over short distances shows no constant relation with the wind direction. Many authors have emphasized this, the latest to do so being Gunn *et al.* (1948). Indeed, the

importance attached to this finding seems rather excessive. A constant relation between wind direction and locust direction could hardly be expected, considering that locusts have been seen flying in winds that ranged in speed from well below to well above the air speed at which the locusts themselves can fly. Nor does the lack of a fixed relation between wind direction and locust direction mean that the locusts are indifferent to or independent of the wind. On the contrary, it is the very variations in this relation which provide the best evidence that locusts respond actively to the wind. The variations are not random, but regularly related to the wind speed and height of flight. This has been discussed elsewhere, in part I; the provisional conclusions reached may be stated very briefly as follows:

Desert Locusts orient themselves actively (probably by optical means) to the wind. Near the ground they fly against the wind unless it is so strong that they can make no headway, whereupon they turn across and preferably down-wind, or settle. At intermediate heights they are oriented only by winds too strong for the locusts to make headway into wind, and so tend to fly down-wind. Higher still they are not oriented by the immediate wind, but inevitably their tracks are biased down-wind.

Assuming that the wind has these effects upon the direction of migrants, the question at issue is whether the effects could create long-range directional movements. Before this question can be answered we must consider to what extent long-range migrations really are directional. As already stated, the mapping of swarm reports shows that movements are by no means directional in the sense of there being uniformity of flight direction among all the swarms involved in a given trend. And single swarms have often been seen to change direction even within the short period they could be kept in sight by fixed observers. Further information on this point has recently been provided by the unique observations of Gunn *et al.* (1948), who were able to locate the roosting sites of two swarms for many successive nights. The roost-to-roost directions changed from day to day, each complete track zigzagging and even sometimes doubling on itself. In each case, nevertheless, a considerable *resultant* displacement of the swarm had occurred in a certain direction by the end of the period. Flight at higher levels, or over the sea, or in gales, may result in very extensive movements in one direction. But Rainey & Waloff (1948), who selected for study just such flights, produced good circumstantial evidence that even they occur in varied and changing directions in the same period and region. It is rare to find a number of swarms moving in the same direction day after day (for examples of this, see pp. 275–276). On all the available evidence, we must visualize most extensive swarm movements as made up of resultant displacements which emerge from a complex of variable movements and which, when sufficiently large and sufficiently alike among a number of swarms in the same season and region, add up to a long-range trend.

Clearly, the consistency of direction seen in a long-range trend is a very different thing from the stability of direction so characteristic of migrants as seen at any one place. Over short distances and periods (from seconds to minutes and even, on occasion, perhaps to hours) the direction of flight of migrants is strikingly constant. The causes of this have been discussed elsewhere (Kennedy 1945 and part I) and are believed to include ‘gregarious inertia’, the sun-compass reaction and other behavioural consequences of the migrant’s locomotory ‘drive’. But none of these direction-stabilizing agents appears to have any lasting action. They are essentially stabilizers of the direction of the recent past, in whatever

way that was determined. Passing to consideration of flights over rather longer distances and periods (from minutes to days), the constancy of direction tends to disappear. And the wind, in particular, often impresses the observer as a main cause of the directional irregularities he finds; the very opposite of a direction-stabilizer. Generally speaking, it is only when we consider flights over even longer distances and periods, and among a number of swarms, that directional consistency emerges again, in the resultant form described.

Hence long-range migration trends are not simple extensions of short-range movements in a fixed direction, but represent a new, higher-order form of directional consistency. If so, the possibility remains that long-range directional consistency is after all determined by the wind, although the wind is often the enemy of short-range directional stability.

In the behaviour analysis (part I), attention was naturally concentrated on what the locust itself did when stimulated by air movements. But the moving air does more than provoke reactions; it is at the same time the locusts' medium, it bears them. Indeed, on the optomotor theory, it is because the wind bears them that it provides stimuli to which the locusts respond.

The moving air is constantly tending to carry the locusts 'passively' over the ground, that is, independently of their flight exertions and orientation. The resultant tendency of the locusts' whole behaviour, on the other hand, is to make that displacement (their *track*) reflect only the locusts' own exertions and orientation (*course*). *In short, there is a constant struggle between locust and wind for control over the locusts' displacement.*

It has been pointed out (part I, p. 259) that the key to the migrant's behaviour is its irrepressible locomotion. The other peculiarities of its behaviour can be traced to its locomotory 'drive', being expressions of the well-known, sensory-stabilizing tendency of nervous reactions, now operative in the special context of constant locomotion. In other words, the migrant's reactions tend to minimize the sensory disruption created by its own locomotion. Seen in perspective, the struggle between locust and wind for control over the locust's displacement is merely one aspect of that essential contradiction between the migrant's two powerful tendencies, movement and sensory stabilization.

The word 'control' is used in this connexion in a strictly objective sense. A locust is defined as having control over its own displacement when, that displacement being apparent to it, it keeps its ground speed at or below its air speed and its track close to its course. Keeping control in this sense is an outcome of the insect's preference for a certain retinal velocity and air speed; the locust keeps control (i) by energetic flight, (ii) by commonly flying low enough, and in sufficient light, for its speed and direction with reference to the ground to remain apparent to it, (iii) by orienting itself with reference to that apparent movement, and (iv) by descending and settling when the wind speed exceeds the insect's maximum air speed.

So long as the locust is able to keep control in this way, its ground speed will be rather low (not exceeding its own airspeed) and *its track will have an up-wind tendency*. The latter will not be more than a tendency, for locusts fly even when there is so little wind that the locusts' control over their displacement is virtually complete without their having to orient on the wind. But since they fly also in stronger winds, when control can be maintained only by active orientation, it may be said that flights under the locusts' control will have an up-wind bias. And in the absence of an overriding bias in some other direction, the up-wind bias will

create an over-all tendency to up-wind displacement among self-controlled fliers. The strength of the tendency will increase with the strength of the wind.

The situation will be quite different if the locusts lose control over their own displacement. A locust is defined as having lost control over its own displacement when, that displacement being no longer apparent to it, it is unable to keep its ground speed below its air speed and its track close to its course. Loss of control will impose a down-wind tendency on the locusts' tracks. Again, this will be no more than a tendency, for locusts fly when the wind speed is much less than their air speed so that their tracks can be up- or across-wind, even if they are not actively controlling their own tracks because they are flying high, or in the dark, and cannot see the relative movement of the ground. But locusts fly also in stronger winds, and it is obvious that the displacement of any air-borne insect not showing a sustained preference for up-wind orientation must develop a down-wind bias, if the wind speed and the insect's air speed are of the same order. Furthermore, locusts exercising what may be termed partial control, that is, flying in winds too strong for them to make headway but high enough to maintain their preferred retinal velocity and air-speed by turning down-wind, will then move down-wind at the maximum possible ground speed for the given wind speed. Thus loss of control creates a down-wind bias which will, in the absence of an overriding bias in some other direction, create a pronounced tendency to down-wind displacement. Again, the strength of the tendency will increase with the strength of the wind.

If locusts in control of their own displacement have a tendency to move up-wind, and those that have wholly or partially lost control have a tendency to move down-wind, we have here a possible basis for the creation of trends, and the crucial question then becomes: what, in turn, determines the amount of control the locusts have over their own displacement?

The principle of 'rectification'

An example of a trend created, apparently, by externally imposed changes in the amount of control exercised by the insects over their own displacement, is provided by Beall's (1941, 1942) observations on Monarch butterflies (*Danaus plexippus* L.) on the northern shore of Lake Ontario. This case has several advantages as a first example of trend-creation. The whole process was observed at one place, an exceptionally favourable circumstance not yet encountered with locusts (although very similar behaviour has been observed in locusts, see part I, p. 192). Secondly, Beall's observations were made in the autumn when these butterflies are seen migrating southwards over a great part of the North American continent (Williams 1949 *et ante*). The specimens Beall watched moved southwards out over the lake whether the wind was blowing from north or south, which might be regarded as evidence of a directional urge driving the insects southwards regardless of the wind. Yet the unusually full account Beall gives of what he saw permits of a different interpretation. If so, his work deserves particular attention because the idea of a directional urge, derived from the study of butterflies, has been applied to other insects including locusts (Williams 1930, 1942).

Beall observed that with a wind from the north some butterflies flew northwards against it, keeping very low over land and water. But at the same time a larger number at a greater height were drifted southwards over the water by the wind while still headed northwards. With a wind from the south all insects seen flew southwards against it, keeping low over the land and water; higher fliers were not seen. These observations show that the southward

trend was not due to the butterflies being under an inner compulsion to fly that way. The winds from north and south, so far from being merely incidental features of the situation, were actually responsible for the majority of migrants moving always in the same direction, southwards from shore to lake.

This persistent off-shore trend falls into place alongside other observations on insects in wind, if we assume that the insects respond to the apparent movement of their visible substrate. There is evidence for that assumption (Kennedy 1940, and Part I), and, if it be correct, the off-shore trend can be attributed to the fact that the 'maximum compensatory height' is greater over land than over water. In other words, the relative movement of the ground due to the insects being carried over it by the wind remains sufficiently

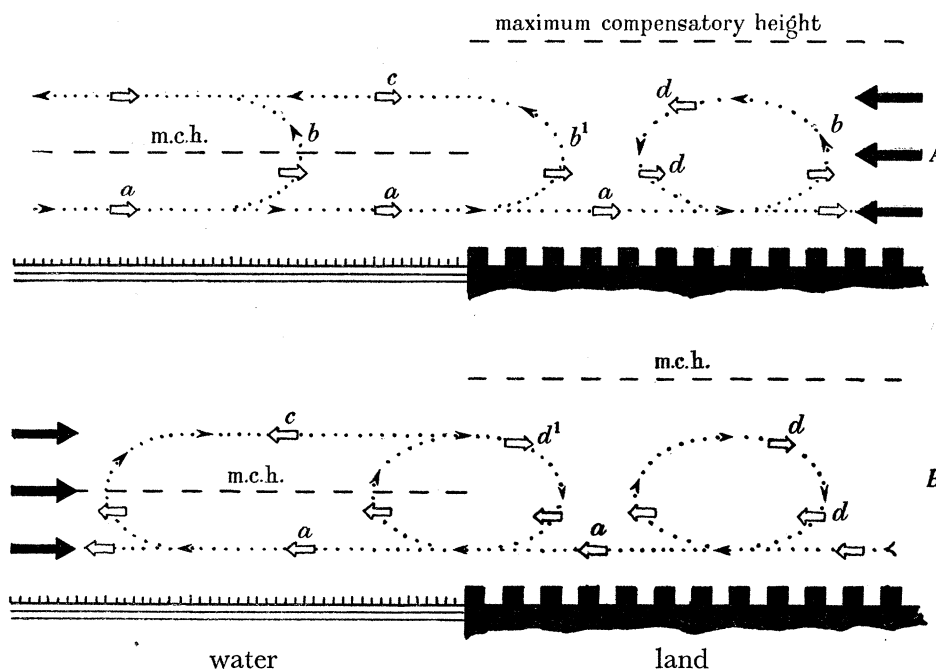


FIGURE 14. Diagram of the postulated 'rectifying' action of a land-water junction upon the movements of flying insects, based on the optomotor theory of behaviour in wind and the observations of Beall (1941, p. 127) on *Danaus plexippus* L. Resultant movement is from the land out over the water, both when the wind (heavy black arrows) is blowing off the land (A) and when it is blowing off the water (B). Outline arrows: orientations of insects; dotted lines with simple arrow heads: paths of insects. Further explanation in text.

apparent to them to evoke orientation and height-varying responses, at a greater height over land with its profusion of large landmarks, than over water with its finer, more uniform, visible pattern.

The probable course of events is best described by reference to figure 14.

When the wind is from the north (off-shore) (figure 14A) low-fliers will respond to it and so make halting progress up-wind, northward, over land and water (aa), rising in the air during calmer spells (bb). When the wind speed increases to above their air speed, fliers below the maximum compensatory height will soon turn down-wind and descend, to settle or to resume their slow up-wind progress in the weaker wind close to the ground (dd). The maximum compensatory height for any given wind speed is greater over land than over water. Many higher fliers that are hit by a wind gust while below the maximum compensa-

tory height over land (b^1) will start the responses (descent, etc.) which would ultimately arrest their down-wind displacement, but will find themselves over the water (c) before these responses have succeeded in arresting that displacement. Over the water, the insects will now be above the maximum compensatory height, will cease to respond and will be carried farther and farther on the wind. The opposite, up-wind, northerly movement is slow, being arrested and even reversed by every gust. The resultant displacement will be southward, with and on the wind, because once over the water the insects' ability to resist carriage by the wind is drastically reduced.

When the wind is from the south (on-shore) (figure 14*B*) low fliers (aa) will make halting progress up-wind over land and water as before. As before there will be only a limited amount of carriage of higher fliers by the wind over land because the maximum compensatory height is great and the insects' responses to being carried down-wind soon arrest their down-wind displacement (dd). As before there will be relatively free carriage even of only moderately high-fliers over water (c) where the maximum compensatory height is small. With-wind displacement will, however, be limited, for the simple reason that it will quickly take the insects over the land (d^1) where they can stop it. The resultant displacement will be slow but southward, into the wind, because the wind's tendency to carry the insects with it is restricted, leaving the insects' contrary tendency to move up-wind predominant in effecting their displacement.*

Thus the persistent off-shore trend arises because when the wind's direction reverses from on-shore to off-shore, its effect on the insects' resultant displacement also reverses. A full interpretation of Beall's observations would require consideration of other points, such as the relative strength of northerly and southerly winds, the insects' probably unequal readiness to alight on land and water, the lack of wind-braking obstacles on water, and so on. But these are ancillary points which do not affect the principle involved.

The action of the land-water junction on the displacement of the insects may be likened to that of a valve; it encourages displacement in one direction but hinders it in the other. There is no English verb-form of the word valve, to describe the action of the land-water junction, so it is proposed to borrow the term 'rectify' as a verb used in a similar sense in the terminology of electrical circuits.† This particular rectifying effect has been observed in both butterflies and locusts, but can hardly be of first importance in creating the migration trends of either. But, if there are other and commoner ways in which the locusts' control over their own displacement is enhanced or weakened in a systematic manner, then the rectification principle may be of real importance as a means of long-range trend-creation.

* Dr W. H. Thorpe has pointed out to me that an on-shore wind would tend to accumulate resting insects along the shore, by this same action that causes flying insects to move out from rather than in toward the shore. This action may help to build up the assemblies of Monarchs observed not only on the shores of the Great Lakes but also on the Southern California and Florida coasts.

† No close parallel is meant with any of the numerous devices by which circuit elements are arranged to 'rectify' alternating currents. The term is used here to designate a natural process of a type that is most difficult to cover with a single term. A special term is necessary because this type of process, of which rectification is but a special case, is common and quite distinct, viz. the establishment of an overall pattern from elements that are not *in themselves* responsible for it, but become so by virtue of their particular interrelationship. Thus rectification is the process by which a behaviour pattern, in itself capable of producing movement in a variety of directions, is transformed into an essential causal element in the production of movement in one particular direction. I am particularly indebted to Mr D. R. Newth for constructive criticisms here.

'Rectifying' agencies

Locusts retain control by flying near the ground and settling when they cannot make headway against the wind. If they persist in flying when they cannot make headway or fly too high to see they are being transported, they lose control, which passes to the wind. It follows that *anything tending to restrict the amount and height of flight tends to keep courses and tracks up-wind and ground speeds low. Anything tending to increase the amount and height of flight tends to make courses and tracks down-wind and ground speeds high.* Agencies which affect the amount and height of flight (or the visibility of the substrate) thus become *rectifying factors*, theoretically capable of creating long-range directional trends of migration. Such agencies are not difficult to find. Evidence that the various environmental influences affect migrant locusts' behaviour in the ways to be described below, has been given in part I.

Various aspects of the *wind* itself are manifestly rectifiers. Take first those aspects which favour locust-controlled displacement, that is, movement against the prevailing wind. They are: wind speed generally low, seldom exceeding 5 m./sec., and wind direction steady; in other words settled weather without much interference from storms or strong winds. Such were the conditions in south Iran in spring, 1943, when migration, both as observed directly and as deduced from the shift of swarm populations across the map, was against the wind and rather slow. Winds were often negligible at the time of observation and the migrants were often flying well above the ground, probably beyond the maximum compensatory height. But conditions of steady and weak winds are clearly also those giving the maximum opportunity for the stabilizing factors to maintain an orientation only intermittently imposed by the wind. Under such conditions the orientation assumed at the morning departure from the roosting site would have a good change of survival for hours.

It is suggested that the striking observation of de Lépiney's (1928) in Morocco comes within this category. Both adults and hoppers migrated consistently to north-north-east for 6 days. This might perhaps be explained as follows. Both hoppers and adults first oriented perpendicularly to the rays of the morning sun while basking before migration started. Some would of course be facing roughly south and others north at this time, but when migration began the balance was tipped in favour of the northward orientation by the wind blowing from the north-east (this sequence of events was observed in Kenya on 13 May 1944; part I, p. 172). The locusts moved off north-north-east, their orientation maintained through wind lulls, temporary changes in wind direction and when the locusts were above the maximum compensatory height, by gregariousness and probably the light-compass reaction.

Unless the wind direction be steady, as well as its strength moderate, up-wind migration may lead to a series of moves now in this direction and now in that, amounting to little or no geographical displacement over a period. In a season of light winds of variable direction such up-wind flight as occurred would thus not bring about any major geographical displacement. This may be one reason, among others, such as cold, reproductive behaviour, etc., for the confused periods between periods of major migration movements.

Wind conditions which tend rather to deprive locusts partly or wholly of control over their own displacement, and so to favour with-wind movement, are of several kinds.

First, when the wind continues very violent and gusty, locusts can be swept away with it (part I, p. 183). Even if the locusts remain below the maximum compensatory height they go on being carried, and oriented, down-wind because they are 'goaded' into

persistent flight. That may occur only once or twice in a season but can be overwhelmingly important in terms of geographical displacement. The sudden, short, but critically important eastward moves in the Arabia-Persian Gulf-Baluchistan area in spring 1943 and 1944 appeared to be brought out partly by these means.

Secondly, when the wind begins by being weak, say first thing in the morning, thereby encouraging the locusts to rise high, and then strengthens, it will carry the locusts with it, although without orienting them while they are above the maximum compensatory height. This unoriented carriage of high-flying locusts probably occurred during the gale periods mentioned above, and it may be an important cause of with-wind geographical displacement whenever high-flying occurs, as during the evacuation of summer breeding areas.

Thirdly, when sudden bouts of strong wind alternate with periods of weaker wind against which fliers can make headway, the resultant movement can be down-wind, even below the maximum compensatory height. The function of the periods of weaker wind as contributors to that resultant movement is to ensure that the locusts become exposed to and oriented down-wind by the strong wind below the maximum compensatory height, although they may eventually be brought down by it. Sudden lulls in the wind which stimulate taking-off will have the same function. This state of affairs was observed in Kenya in 1944 (pp. 183, 202). The swarms were observed usually flying up-wind, although often with difficulty, and this meant a variety of flight directions owing to the variable winds of the broken country. The swarms certainly did not give the impression of a steady northward trend, although the prevailing wind at that season is from the south (Brooks & Mirrlees 1932), and the resultant displacement of swarms during the period was definitely in the same direction, as in previous years (Waloff 1946*a*). From observations and from inference the slow up-wind migration flights could not determine the direction of resultant displacement, for during the brief periods of strong wind blowing to north or north-west, the locusts covered disproportionately large distances. The up-wind flying in variable directions delayed but did not prevent the northward displacement. The main reason for the down-wind displacement was the variability of wind speed. The locusts were able to get well into the air during the periods of moderate wind, and were then 'whisked away', oriented down-wind, for some distance before they were induced to settle.

Fourthly, consider locusts flying at an intermediate height above the ground, where their retinal velocity reaches the compensatory threshold only when the wind is already strong enough to impose down-wind orientation, but is below that threshold when the wind is weaker and would permit up-wind progress. A moderate wind will not orient this swarm. But when a gust of air moving faster than the minimum compensatory speed hits the swarm, the locusts will orient down-wind; the more readily if they are dense enough for gregarious reversal to occur (see part I, p. 229). When the wind drops again to less than the minimum compensatory speed, it will not cause the locusts to re-orient up-wind. Observations of swarms being thrown into confusion and turned down-wind on meeting gusts and storms, or flying persistently down-wind in front of advancing storms (p. 202), suggest that this sequence of events may be of considerable importance in rectifying geographical displacements. It may have contributed to the with-wind displacement of swarms in Kenya (above).

Thus the wind itself appears to be an important rectifier. Its speed and structure, and systematic variations in them, affect the amount and height of flight and rectify the wind's directing influence, causing swarms to shift across the map now with and now against or even across the prevailing wind, or to move hither and thither with but little resulting displacement on the map.

Temperature may be a very important rectifier, although further information is greatly needed on this point. Hot, sunny weather probably increases the amount of flying done and so reduces the likelihood of the locusts settling when the wind is too strong for them to avoid being carried by it, lengthens the daily duration of flying (which may then extend into the night), and increases the average height of flight whether by inducing the locusts to rise by their own efforts or by creating powerful upward convection currents (Rainey & Waloff 1948). Cool, cloudy weather probably leads to flying at lower levels and for fewer hours per day. High temperatures would therefore favour with-wind displacement; low temperatures would favour up-wind flying, often with too little overall displacement to create any major trend (part I, pp. 238–239).

Dryness, whether of the air, of the insects or of both, may act in much the same way as high temperature, but its role in the behaviour of Desert Locust swarms is uncertain and seems to be less important than for some species (part I, pp. 246–249).

The configuration of the *visible substrate* may produce a variety of rectifying effects. The direction of *mountain valleys* may create trends (like the year-round trend along the Ethiopian part of the Rift Valley (Waloff 1946*a*), or the movement up the valleys running north-west in south Iran in spring), by canalizing winds or guiding the insects visually (p. 245) or both. The change of visible background at a *land-water junction* could act in two distinct ways on the optomotor theory. Sometimes, perhaps when the water looks strikingly different from the land (sky reflexion, foam, etc.), or when the beach itself forms a conspicuous break in the visual field, the shore can act as a barrier, and swarms coming from inland turn and move along it (p. 198). On the other hand, a land-water junction also acts as a wind-rectifier, not through the visual influence of the junction-line itself, but probably because of the absence of visible 'landmarks' on water. The shore-line then has a local wind-rectifying effect favouring displacement from land out over the water when the wind is both off-shore and on-shore, as already described (pp. 267–269). Wind rectification through failure of wind orientation and height 'control' over water may have important long-range effects as well. Other things being equal, locusts will have a more pronounced down-wind tendency, and will move faster, once they are over the sea than they do over land. That may well be one reason why Rainey & Waloff (1948) were successful when they assumed down-wind movement, in interpreting swarm movements over the Gulf of Aden, even if some of their assumed heights of flight were too great.

Any other circumstances that eliminate wind-induced background responses, e.g. night migration, would also favour long-range, with-wind displacement. Note that night migrations are reported (part I, p. 234) in end-of-breeding-season periods of hot, desiccating weather, periods when swarm displacements are most clearly with the prevailing winds (Rao 1942; Waloff 1946*a*). Such weather can rectify the wind's directing influence, therefore, not only by causing high flying by day but also by causing night flying and so bringing another factor, *light*, into operation.

The *age of the locusts* themselves is a rectifying factor. Young *fledgling* locusts seem to respond to wind in the same way as fully hardened ones, but their physical ability to make headway against it is less (p. 200). This should favour down-wind geographical displacement of fledglings, even when the conditions enable older locusts to maintain an up-wind orientation and hence to show either an up-prevailing-wind trend or no trend at all. It seems to follow that fledglings could never make a major migration movement against the prevailing wind, for when low enough to orient up-wind they are too often grounded by the wind. Given warm, calm periods encouraging them to rise well away from the ground, however, they could be displaced long distances down-wind. This probably accounts, in part, for Waloff's (1946*a*) finding that the down-wind trend of migration among *Schistocerca* swarms in East Africa was most clearly defined when new adult swarms were appearing at the close of a breeding season. Conversely, the displacements of fully hardened older locusts not occupied with reproductive activities, would be rectified up-wind as Waloff also found.

Bearing in mind that all these rectifying factors can operate at the same time in varying degree, it is obvious that the possibilities of trend-creation are rich and varied.

Williams (1930) and Key (1942) have suggested a different form of rectification: that the sense of the insects' reactions to wind may depend upon the temperature or humidity or some other condition of the wind. Key's records, for instance, suggested some preference for the movement against the wind, but an even clearer preference for movement up the geographical humidity gradient. He suggested that a change in the humidity of the immediate wind might reverse the sense of the insects' orientation on the wind. But there is no evidence of a direct reversal of the wind reaction itself, and there is no need to postulate it (part I, p. 248).

An access of moisture in the air causes desiccated *Dociostaurus* to fly, to keep low and orient into wind (Bodenheimer 1944). A change in the humidity can, therefore, reverse the course and tracks of the insects relative to the wind, not by reversing the reaction to wind, but simply by evoking a latent wind reaction or by changing the amount and height of flight. Key's data do not include the details necessary for deciding whether the different humidities of the winds, or their different strengths, or some other differences, were the essential rectifying element for *Chortoicetes*. But the form of rectification considered by him and Williams, in assuming that elements like temperature and humidity effect trend reversals by inducing the insect to reverse its reactions, places all the responsibility for the trend-creation on the insect, an unnecessarily complicated hypothesis as to its behaviour. This theory overlooks the fact that insect-wind relations already provide a basis for trend-creation and trend-reversal, so that elements like temperature and humidity can have a positive but indirect trend-creating influence.

ESSAYS IN THE INTERPRETATION OF ACTUAL MIGRATION TRENDS

Until continuous observations on behaviour and weather have been made we shall not know how far the various suggested rectifying processes are in fact responsible for the migration trends revealed by cartographical methods. Meanwhile, some essays in the interpretation of actual migration trends will serve to illustrate the suggestions made.

Consider first the trends prevailing during the two main periods of the writer's observations, and already tentatively analyzed as far as the wind's own rectifying action alone is concerned (pp. 270 and 271). In Iran in spring, 1943, the displacement of the whole swarm population was northward and north-westward as judged from mapping of the records. The winds were observed to be predominantly from the same quarter, which is normal according to Bauer (1935). The most frequently observed direction of flight was against the wind. Instances of sustained down-wind flight in stronger winds were exceptional. Although such brief flights are easily missed, it was not thought they were frequent, as the weather was clear and settled and winds seldom strong. The whole trend seemed to be due to up-wind movement.

The trend of swarm displacement was again northwards in the Kenya highlands in spring, 1944, but otherwise conditions were very different. The weather was much less settled. Wind directions noted at the time of locust observations were inconsistent and affected by the irregular relief. The observations were too few for a good estimate of average wind direction, but according to Brooks & Mirrlees (1932) the prevailing wind is southerly at that season—that is, with the migration trend (Waloff 1946*a*) instead of against it. Low-flying locusts were observed moving usually against the wind as in Iran, but there were more cases of flight not apparently related to the wind direction on the ground, reflecting the more disordered state of the air currents. The general picture was of swarms frequently changing their directions and tending southwards rather than driving steadily northwards as in Iran. Thus the Kenya highlands act as a temporary trap for swarms entering them, not merely because the cool, cloudy conditions reduce flight activity (Waloff 1946*a*), but also because they keep flights low and so confused in direction. As in Iran, cases were observed of sustained down-wind flight in stronger winds. On these occasions the wind was from a generally southerly direction. Although the proportion of total flying time occupied by these with-wind moves was relatively small, only they were capable of creating a geographical trend because movements made during the rest of the time were chaotic or ineffectually up-wind.

Note that the difference between the Iran and Kenya trends—the former against and the latter with the prevailing wind—is attributed to the *combined* effects of temperature and wind structure. Skies were clear in Iran, and it was warmer than in the cloudy Kenya highlands. If this had been the only difference between conditions in the two places the migration trend should have been more clearly up-wind in Kenya than in Iran. The swarms in Iran were often enabled to rise high, probably often beyond visually-responsive range of the ground, by the warm weather during the day. Yet they maintained their up-wind orientation because it was not disrupted by gusts or storms. The warmth enabled them to fly for many hours daily. So their up-wind flight became a major geographical trend, given the steady wind direction. Indeed, the very fact that they often rose well away from the ground may have aided their up-wind displacement because they were not grounded by small temporary wind increases. The swarms in Kenya were held closer to the ground which ensured up-wind orientation when they did fly, but the wind directions were variable, flying was often interrupted by gusts and daily flying hours were restricted by cold and rain so that up-wind flying did not create a trend against the prevailing wind. On the contrary, the cooler, cloudy conditions, given the gusty winds, created a with-wind trend. Although

the proportion of the total flying time occupied by with-wind moves was small, these moves were nevertheless so rapid and covered such relatively long distances that they were responsible for a resultant, northward, with-wind trend.*

It appears, therefore, that, although swarms may spend a great deal of time flying against the wind, this can develop into a long-range up-wind trend of migration only under rather exceptional circumstances. The wind must be moderate in strength, otherwise the swarms will advance only to be halted and flung back again, and it must be steady in direction, otherwise they will not advance in one direction. The weather must be neither too cold nor too hot, for when it is too hot swarms will rise too high to orient up-wind, or they will fly at night with the same result. When it is too cold, movement will be too slow for any trend to appear. It is not yet clear how far the migration trends in the spring in Iran and Baluchistan, and in winter-spring in Arabia and north-west Africa, are due simply to flying against the gentle, generally northerly wind, and how far they are assisted by the cyclones that occur at that time (Banerji 1931). Both effects seem to play some part. Invasions of Palestine (Bodenheimer 1932), of Egypt (Egypt 1916; Ballard *et al.* 1932) and of interior Baluchistan (Rao 1942) seem often to be brought by cyclonic winds and sandstorms. On the other hand, the invasion of Palestine in 1929–30 was not aided but halted several times when cold, wet gales blew from the south-west (Bodkin 1931), and steady up-wind flight has been recorded at this season in Sinai (Tristram 1880) and in Iran (see above; also Siyazov 1928). One would certainly expect the cold, flight-suppressing storms of winter-spring to be less effective as creators of with-wind trends than storms in the summer-autumn.

The combined rectifying effects of high temperature and locust age are perhaps mainly responsible for the great with-wind migration trends during hot, dry weather when young swarms are evacuating areas where they have been bred on earlier rains (Waloff 1946*a*; Rao 1942). The swarms are very active, and the predominance of with-wind tracks and courses is probably due to the swarms frequently rising—or being lifted—away from the ground in hot weather. There is, for example, a dramatic reversal of migration trend, both on the map and in relation to the wind, in parts of north-west Africa in the spring (Donnelly 1947). The reversal is associated with increasing temperature and desiccation and with a change in the age of the locusts concerned. In December–May mature swarms move steadily north-eastwards against the prevailing north-east surface wind. In May–June the young swarms of the new generation move in exactly the opposite direction, south-westward with the same north-east wind. The main migrations of spring-bred swarms are generally with the prevailing surface wind also in eastern Africa (south-westwards), in Iran and Baluchistan (eastwards) and south of the Sahara (westwards). Later in the year, when hot, dry weather returns after the monsoon rains, the migrations of the new swarms are again

* The predominantly northward direction found by Waloff (1946*a*) among the swarm reports sent in by casual observers seems at first sight to contradict our finding of a confused, southward tendency in the same area and period. However, the chances of a swarm being reported by casual observers are greatest when that swarm passes over the largest number of observers in given time, that is, when the swarm moves rapidly over a long distance and is fairly well up in the air. Reports from casual observers are thus weighted in favour of down-wind movements, northward in this case. Reports obtained by observers who are actively seeking swarms and whose chances of finding them depend on the swarms not having moved far from where they were last seen, are weighted in the opposite direction, in favour of the lower, slower, longer-lasting, up-wind movements.

with the prevailing winds in eastern Africa (north-westwards), India (eastward and south-westward) and south of the Sahara (eastwards).

However, although the migrations of swarms during hot weather are often with the prevailing surface wind, they may be across or against it, and we have not yet enough information on local weather to attempt even a first interpretation of many of these movements. Sometimes they are due to exceptional, non-prevailing winds acquiring especial importance. Thus the trend of migration among scattered locusts in the northern Sudan and upper Egypt in autumn 1942 was northwards (Kennedy, in preparation), that is, against the seasonal prevailing wind (Sutton 1925, 1930). Observations on some of the moves made by these locusts showed that the winds actually carrying them were associated with occasional, sharp rain- and dust-storms moving northwards. Those locusts were not in swarms and their behaviour was not typical of swarm members, but swarms, too, have occasionally been recorded as moving northward from the Sudan at this season (in October-November, 1927 and 1928), perhaps from the same causes.

As a rule swarms evacuate the Sudan-Eritrean monsoon breeding areas eastwards, roughly with the south-west prevailing wind. This eastward movement continues after surface winds have become northerly. Nevertheless, this later phase is not inconsistent with the heat-rectification hypothesis of these post-monsoon movements, because while surface winds are northerly the upper prevailing wind becomes westerly and the locusts may rise to within the latter's influence under hot, dry conditions.

The rapid eastward movement across Arabia and Iran into India observed in spring 1942 and 1943 (part I, p. 183) was also across the prevailing northerly wind. This movement did not result from the locusts rising into an upper wind differing in direction from the prevailing surface wind. The surface wind itself changed to westerly for a few days and was then exceptionally violent, hot and dry. The locusts were too stimulated to stay on the ground and effected a prodigious geographical displacement toward an area of summer rainfall, a movement of crucial importance for the further progress of the migration and breeding cycle. The temperature, wind speed, wind structure and perhaps also the dryness of the air, all probably conspired to rectify the locusts' movement down-wind in a spectacular manner. Before and after this short period they were migrating steadily northward in Iran, and went on doing so into the summer, although unable to breed and destined to disappear there. Faure (1894), Regnier (1926) and Bodenheimer (1932) are among those who have also spoken of Desert Locust invasions being brought by winds that were both hot and violent.

One quite exceptional migration movement has been interpreted in the light of the detailed meteorological situation by Waloff (1946*b*). This was a rapid movement of *Schistocerca* swarms from the westernmost point of Africa (south of Agadir) to Portugal and Spain in October 1945. She suggested that the high temperature over the land at the point of origin enabled the swarm to rise to 1500 to 2000 ft., where there was a 30 m.p.h. southerly wind capable of carrying them to Portugal in the time available. She suggested that their estimated average speed of 23 to 28 m.p.h. could not have been achieved at the surface because the wind there was generally less than that speed. It should be pointed out, however, that if the locusts were oriented down-wind they might have maintained the necessary average speed even at the surface. Moreover, if they were down near the water

in daylight in a wind too strong for them to make headway, they probably would in fact be orientated down-wind, especially if dense enough for gregarious re-alignment to occur.

Bearing in mind that swarms have been said to average only 20 to 30 miles a day over land, Waloff suggested that it was simply the act of flying high in the rapid wind which enabled the locusts to cover so great a distance in one day or so. Another reason that may be suggested for the locusts flying so far and fast was that they were over the sea, and not over land. It seems probable that the high temperatures over the land enabled the locusts to rise high and so cross the coast, but there is no evidence that they remained high throughout their long journey. The locusts were reported in Portugal mainly near the coast itself. They were flying now southwards, against the wind. This also suggests they were low before reaching land and had changed their behaviour on arrival over land simply because they could now see the substrate's apparent movement. It is not apparent how descent could have been induced merely by a decrease in wind strength, as Waloff suggested.

The above analyses are tentative. What is required is the study of individual trends according to the actual weather at each time and place. Without more information it is not possible to offer even tentative explanations of some well-defined across-prevailing-wind trends, like the north-westerly movement across the Sahara in October-January which occurs when the prevailing surface wind is north-east.

Nevertheless, the various 'rectification' hypotheses do show some promise as means of interpreting actual migration trends. The immediate conclusion from these interpretative essays is that the great migration trends, which are roughly with or against the prevailing wind, emerge from the mesh of migratory movements *only when several rectifying influences are acting together in the same sense.*

DISCUSSION

'Active' versus 'passive' migration

The theory advanced here attributes long-range movements to both insect and wind acting together. Most writers on insect migration have sought rather to separate the action of the insect from that of the wind. They distinguish active or 'voluntary' migration from passive or 'involuntary' migration. This conception has been carried to the extreme by Acworth (1940), who divides all insect (and bird) migrations into two neat stages, an outward drift on the wind followed by an active 'homing' flight. Acworth's simplified theory has won little support, but the distinction between active and passive migration is made also by Williams (1930), who regards passive migration as typical of some insects, but takes the view that it should not then be called migration. The term migration he would reserve only for the active (that is, powerful) migrants, such as butterflies, dragonflies and locusts. He does not say that the displacement of true migrants is invariably due to their own exertions but, even when it is passive, he regards it as under the continuous control of the migrant:

'The movement is produced, to some extent at least, by the efforts of the migrating animal, which is neither a passive victim of overpowering external forces nor an active objector to them.'

And, more specifically:

‘The migrating animal is in some way conscious of, and helps to determine, the direction of movement.’

Thus the view that migration is essentially active has been developed into a theory of consciously directed movement.

Analysis of the behaviour of migrant locusts (part I) shows they are subject to an internal ‘drive’ that makes them fly, but that this is not a geographically directed drive. The most decided trends of locust swarm migration are with the wind and appear when the locusts have *least* behavioural control (in the objective sense defined on p. 266) over their own displacement over the ground: their main contribution is to keep flying. Vice versa, trends become confused or even disappear when the locusts have nearly complete control over their own displacement. A major trend can occur under the behavioural control of the locusts, but only, it is suggested, against the wind. Such a trend is not executed in spite of the wind, but is created by it.

Moreover, it is the ‘uncontrolled’ migration trends that are usually ‘successful’ in the sense of leading to new breeding grounds, while the controlled ones are sometimes ‘abortive’ (p. 276). And migration goes on even among sexually exhausted swarms until they die out (part I, p. 200). It is impossible, as Uvarov (1928 *et seq.*) has always insisted, to entertain the idea that migrations are directed to a goal.

In his more recent writings, Williams (1942, 1949) no longer suggests that the theory of an innate sense of direction can be the basis for further work. He believes (1949, p. 84) ‘the answer will be found in the field of biology and physics’, and that there is ‘a mystery in the sense—and only in the sense—that we have not yet found the answer’. Nevertheless, he adheres to his sharp distinction between active and passive migration, and gives this new definition of the former (1949, p. 70):

‘A change of location which is determined both in distance and direction by the insect itself, and not a passive distribution of individuals by overpowering forces such as strong winds.’

On this definition many of the most spectacular long-range movements of locusts—movements, moreover, which are of crucial importance for the completion of their annual breeding cycle—are not migrations at all, because the wind probably contributes more than do the locusts to their actual displacement over the ground. But, as we have seen, it is only because the insects take to the air so persistently and react in various definite ways that they so commonly expose themselves to carriage by the wind, and by winds from some directions more than by others. Getting into a position to be so carried must be included among the means by which migrants determine—in an objective sense—their own displacements both in distance and direction, along with other means such as orientation. During the period of carriage by the wind, the insect’s displacement is certainly passive from the point of view of a fixed ground observer. But the movement as a whole is nonetheless self-directed in the objective, resultant sense, and if that kind of self-direction is to be excluded by definition, then what remains can only be some kind of subjective, conscious self-direction.

The contrary theory, that long-range migration is essentially passive, has been put forward by Felt (1928, 1938):

‘...winds, especially those of the upper air, are ample to account for the occasional and possibly somewhat general extended movements of insects. There is no necessity for limiting such movements to species possessing superior flying ability since the probabilities are that the purposive flight of an insect—the distance covered by its own efforts—is relatively insignificant’ (1928, p. 123).

There is an attractive mechanical simplicity about this theory, which discounts (without having to deny) a purposive element in migration, and seems to justify treating the insects, for working purposes, as inert particles. Attention is thereby shifted from the behaviour of insects to the behaviour of air-masses. Yet migration remains a biological problem which cannot be solved in primarily physical terms.

More important than the difference between the ‘active’ and ‘passive’ theories of insect migration is what they have in common: the assumption that active and passive migration are alternatives. The one theory holds that a movement is not a true migration unless the insects are in complete control of it; the other holds that insects rarely have any control over their long-range movements which must nevertheless be admitted to be migrations. More commonly, perhaps, these two extremes are avoided, as by Fraenkel (1932) and Freeman (1945), but the sharp distinction between the alternatives of active and passive migration is still retained:

‘...a rich aerial fauna, consisting of weak-flying insects of small size and high buoyancy... These forms, being carried involuntarily by the wind, are dispersed by air movements as contrasted with the migration of moths, butterflies and locusts, which are sufficiently powerful to maintain their flight if necessary against the wind’ (Freeman 1945, p. 150).

What seems to be under-emphasized here is that long-range movement, no matter to what degree controlled *en route*, rarely occurs unless the insects’ behaviour contributes in some positive way to it, and that it is the making of this contribution, not the mechanism of their horizontal displacement, which distinguishes the insects biologically as *migrants*. *Displacement* may be active or passive, but ‘passive *migration*’ is a contradiction in terms.

There is, in fact, wide variation in the degree to which migrants traverse the ground through their own exertions, or on the wind. The variation is continuous and its causes need to be studied; whereas it tends to be left on one side when migration is regarded either as essentially active, or as essentially passive. The antithesis between ‘active’ and ‘passive’ migration is misleading, for it gives primary importance to a biologically secondary matter: the particular *means* of traversing the ground, employed by migrants.

In any given case the antithesis is even more misleading, for activity and passivity are not alternatives. The study of locust migration has suggested that the wind is an essential element in the creation of any geographical trend among numbers of swarms. As long as we are considering such trends, and not the momentary behaviour of a single locust or a single swarm, there is no point at which we can say the insects are now active, or now passive. They are always both active and passive. Swarms can suffer the passive displacement that is the basis of a with-wind trend, only by becoming and remaining actively air-borne. Swarms can accomplish the active displacement that is the basis of an up-wind

trend, only by suffering and successfully overcoming passive carriage by the wind. It is never either the locusts or the wind that creates a trend. It is their conflict which is the basis of trend creation, third factors creating trends by influencing its outcome.

Migration as a complex of interacting factors

Locust students have not, on the whole, been attracted by the 'passive' theory of migration, for they have adequate evidence against it, despite the clear evidence of the wind's importance in long-range locust migrations. They have been even less attracted by the 'active' theory of goal-directed migration, and have emphasized its complete incompatibility with their evidence. But they have not hitherto produced any general theory in place of those they reject, although the material at their disposal is richer in quantity and quality than the material on any other group of insect migrants. Gunn *et al.* (1948, pp. 43-44) have even gone so far as to say:

'The plain fact is that these gregarious locusts migrate in swarms and nothing is known of the causes.'

This was, perhaps, a deliberately exaggerated statement made in order to counter the speculative approach of Heape (1931). But what it implies is that the whole matter is extremely complex, and the best policy is to wait until all the multifarious factors have been unravelled. A preliminary attempt to do that has been made in this and the preceding part. The conclusion is that we are not, after all, dealing with a complex system of 'interacting factors'. In essence, the system is simple.

However fluid and complex the migrations and however many factors might be involved, it was known that order did emerge from the chaos, as a recognizable pattern of trends bearing some relation to seasonal winds. It was plain from everyday observations on locusts and many other insects that they resist carriage by the wind when in a position to do so. These two pieces of information together were basis enough for a first working hypothesis essentially the same as the theory of trend-creation now advanced after much additional work. But they were not so put together by anyone (including the present writer), it seems, because the numerous factors involved were regarded as all of similar rank, although not of similar weight, in their influence on the situation. The tendency was to consider the various factors as interacting, but all direct influences in their own right, demanding patient, piecemeal analysis, without preconceived ideas.

This 'factorial' approach, with its technique of multiple regression, has led to discoveries as in the work of Gunn *et al.* (1945, 1948) on mass departure of swarms in the morning. But the same work showed that main reliance on this approach can mislead the discoverers, when its conventional treatment of events as the product of interaction between directly participating, self-contained factors is projected back into the events in nature. In reality factors like temperature seem to participate in mass departure only indirectly, through their effect upon the relations between individuals, or, more precisely, through their effect upon the rivalry between the individualist and gregarious tendencies of each insect (part I, p. 230).

It seems to have been a similarly mechanistic concept of interaction (and again with the employment of mainly statistical methods) which led to Key's (1942) suggestion that tem-

perature or humidity may reverse locusts' orientation to the wind (p. 273). The temperature or humidity are here assumed to act directly on the insects, reversing their orientation responses to wind. This rather elaborate behavioural hypothesis is unnecessary, since the insects' courses and tracks can be reversed simply by changing the height and amount of flight. There is also evidence (Bodenheimer 1944) that the appearance or non-appearance of wind orientation (but not its reversal) can itself be controlled by air humidity, possibly through changes in the height of flight, which would again help to bias movements up- or down-wind. Thus trends can be reversed without the whole behaviour being reversed, because factors do not act directly or on their own, but in a context; in this case, on an unstable system which itself produces reversals when interfered with.

Williams (1930), while holding the view, rejected by locust workers, that migrants may be guided by an innate sense of direction, nevertheless gave careful consideration to the above hypothesis of long-range direction-determination by direct reversal of orientation to wind.* He shares the mechanistic view of the possible mode of action of external factors, and has merely taken it to its logical conclusion, in the theory of an innate sense of direction. How close to that theory even its intended opponents can come is seen in the final clause of this statement from Gunn *et al.* (1948, p. 44):

'Observation at this stage (stream-away) might therefore provide some indication of the stimuli responsible for the locusts adopting a particular direction, if indeed external stimuli play any part at all.'

Williams has been equally concerned to find external agencies that might determine the direction of migrant insects and was associated with the experimental study even of a rather unpromising agency, the earth's magnetic field (Cockbill 1942):

'I do not think that magnetic polarity is likely to be the cause of orientation—although it is an attractive theory . . . ' (Williams 1949, p. 82).

Magnetic orientation seems an attractive theory only so long as one regards agencies as self-contained, exclusive, direct influences upon the insect, and if, therefore, one's aim is to find some one agency which could guide the insect unremittingly throughout a long-range migration. Since no agency has yet been discovered which seems capable of acting in that way, Williams calls for still further search, and never entirely abandons his alternative explanation: an innate sense of direction. There is, indeed, no third alternative when the environment is regarded as a congregation of self-contained, directly (i.e. reflexly or mechanically) acting factors. It is incredible that such factors would be capable, singly or jointly, of creating a regular pattern of migrations. They are all too inconstant.

Once again, two seemingly opposed theories turn out to be complementary: the one regarding migration as consciously directed and the other regarding it as mechanistically directed. They meet on the common ground of factorial analysis. When the objective approach becomes a purely factorial one, it takes on so strong a bias against having any bias that it leaves an inviting vacuum for subjective theories to fill.

The weakness of the factorial approach lies unnoticed in the very concept of a factor. No matter how much interaction between factors may be recognized, they remain, in this

* He went on to reject this hypothesis, but for reasons (see part I, p. 249) which do not affect the present argument.

conception, self-contained things, like so many billiard balls. Billiard balls can be imagined as having different sizes and weights and as associated in various ways, but they remain discrete, self-consistent things with one set of properties each. When natural forces are thus isolated in thought to distinguish their properties, and then, so to speak, put back into nature by the investigator to see how they interact, they often appear to him still as isolates: self-contained, self-consistent and incapable of behaving in two ways at once.

A natural element, when regarded as a *factor*, is something that varies in quantity *but not in quality*. In order to assess its influence, it is thought sufficient to measure it, and correlate the measurements with the biological events under study. But it is only in idealized isolation that the wind, for example, may be characterized adequately by measurements. As an *influence* it varies both in quantity and quality. The changes in the quality of this influence which come with changes in its quantity, or with changes in the natural context, are the core of the problem.

For example, the concept of self-contained, interacting factors obscures the dual role of the wind in direction-determination. The wind is an element in the central system of locust *versus* wind, yet it is at the same time a rectifying element acting upon that system (p. 270). The quality of the wind's influence in trend-creation varies also with the age of the locusts. To see the influence of a factor it is necessary not merely to measure it, but above all to see the context; otherwise the measurements can even obscure its role.

In our case where displacement of the insects can occur only through the action of two opposed factors, insect locomotion and wind carriage, the other external factors can become influences only as they are focused, as rectifiers, on that antagonism. Even then, the amount and the kind of influence each has, will depend on the others and on the locusts. If such preconceived ideas be admitted, then it becomes possible to suggest a theory of long-range trends without first dissecting out and measuring every element in the complex system and, equally, without abandoning objective analysis by introducing the idea of an innate sense of direction. A trend is not imposed by any external factor but is something new, created by a system in which external factors are causal elements.

The ecological character of long-range migrations

Increasing attention has been given in recent years to the many types of orientation reaction displayed by insects (Fraenkel & Gunn 1940), and this has made itself felt in discussions on migration. It has emphasized the possibility that several reactions, rather than any single one, determine the orientation of migrants (Kennedy 1948; Gunn 1948*b*; Williams 1949). Williams conceded the possibility that the migrating insect might 'orientate at one time by the wind, at another by the sun—and so on', but could see no basis on which the insect's several reactions could be organized into a long-range directional movement, unless it were the insect's own wishes. That conclusion being unacceptable, Williams rejected all known types or combinations of reactions as irrelevant to the problem and appealed for more and more work until the cause of orientation should one day be discovered. Gunn (1948*a*), on the other hand, supporting the idea that migrants are directed by means of more than one reaction, drew attention to the principle of 'multiple assurance' in the maintenance of an upright posture by man, where proprioceptors, pressure receptors, eyes and labyrinths are all used, each of which is adequate by itself.

Neither Gunn nor Williams, however, drew a clear distinction between short- and long-range movements, when discussing how their directions might be set. Unless this distinction be clearly drawn, citation of the principle of multiple assurance may be taken to mean that what is 'assured' by the migrant's multiple orienting reactions is its long-range direction, just as a man's posture is assured by his multiple righting reactions. Williams (1949, p. 84) understood the principle in this sense, and his objection, that this amounts to saying the insect knows the direction in which it wishes to go, is perfectly valid; for how else could the insect's multiple reactions be made to assure one certain direction, for hundreds of miles on end?

But posture-maintenance and long-range direction-determination are not parallel cases. The migrant insect's reactions are not co-ordinated by its nervous system in such a way as to maintain a constant direction over long distances, as a man's reaction-pattern is co-ordinated to maintain his upright posture. The migrant's reaction pattern is co-ordinated in such a way as to do something simpler and more immediate (like posture-maintenance), viz. to maintain the sensed environment as constant as is compatible with the migrant's own persistent locomotion. In maintaining that kind of equilibrium, 'multiple assurance' creates the short-range constancy of direction so characteristic of large migrants (part I). The migrant cannot avoid continuous change in its environment. The best its central nervous system can do toward achieving sensory stability in many circumstances is to keep a straight course, because the changes to which the insect can respond without halting are due principally to its own deviations from a straight course, which produce sudden changes in its relation with the more constant features of its environment. Its reactions are therefore selective in the sense that it reacts to certain more constant environmental features and 'ignores' many incidental features of its moving, panorama environment.

Long-range trends seem to be created quite differently. We know of no environmental feature so constant over long distances that the insects could keep going straight by long-continued, sensory-stabilizing reactions to it. Nor do we need to look for one, since we have no reason to suppose that long-range trends involve flying straight all the way. The basis for organizing the insects' orienting reactions and displacements into a long-range directional movement is not the insect's central nervous system. According to the theory advanced here, it is the environment that selects certain of the insects' reactions (to wind, particularly) and creates resultant trends by means of rectification, while the other orienting reactions make little or no contribution to long-range direction-determination. The large-scale orderliness of the environment, which is of a kind that does not exist on a small scale, is the basis on which the migrants' movements become organized into an orderly pattern of long-range trends. But the environment always acts through the insects' orienting and other reactions many of which are well known, so that all known reactions cannot be treated as irrelevant to the problem.

The theory of an innate sense of direction, and the principle of 'multiple assurance' if applied to long-range directional movements, both assume these are linear extensions of short-range directional movements. The two theories differ, of course, in that the first minimizes the directing influence of the environment while the second insists on it. But they are at one in seeking to explain the directions of both short and long movements in behavioural terms. On the contrary, for locusts at any rate, the fixity of direction seen in short-range movements,

and the consistency of direction seen in long-range trends, appear to be different things, differently created. The long-range trends cannot be explained in behavioural terms alone. They are events on a higher plane than behaviour: ecology. The laws governing the creation of long-range trends, and their organization into a regular pattern, are intrinsically no more elaborate than those governing behaviour, but they are quite different. They are ecological laws, in the sense that they arise from the interaction between a whole population of insects and a whole system of climatic and geographical circumstances. The environment enters into behaviour, one might say, as weather and terrain; but into large-scale migration, as climate and geography.

Migration of other insects

How far the principles suggested here may apply to the long-range migrations of other insects is a matter for investigation. The object of the following remarks is simply to indicate that there is nothing in the evidence known to the writer concerning other insect migrants, which would rule out the extension to them of the general principle of 'rectification', and the consequent distinction between the behavioural and ecological levels of migration analysis. Apart from the fact that some of the alternative theories criticized here have been applied to locusts and butterflies alike, there are already indications that the principles governing butterfly migration may not be as remote from those suggested for locusts as has been supposed.

First, Wiltshire (1946) has pointed out that Lepidoptera migrations, when observed within their 'geographical headquarters', follow a complicated pattern:

'The general picture is one of travel in many directions under environmental stimuli and of temporary or permanent settlement wherever the environment permits.'

The over-simplified picture of an emigration followed by a return as the set pattern of butterfly migration arises, in Wiltshire's view, from the fact that most observers of Palaearctic butterflies reside, not in the headquarters region of these species, but at the extreme edge of that zoogeographical zone.

Secondly, the records already assembled by Williams (1949 *et ante*) show a clear preponderance of migrant butterfly flight directions against or with the wind rather than across it. This he dismisses as mere coincidence, or as due to a 'psychological error' on the part of observers. It must be admitted that such crude statistics are not reliable evidence of any real preference on the part of the migrants. But neither are they evidence against the existence of such a preference. The data, aggregated without regard to the varying and often unrecorded circumstances at the time of observation, do not permit any allowance to be made for wind speed and height of flight. This procedure would conceal the sort of consistency in flight direction-wind direction relations found with locusts. What can, therefore, be safely said is that the available data in no way exclude the possibility of the wind having an important influence on the direction of butterfly migration, but an influence that changes according to the circumstances as with locusts. The mainly statistical approach to butterfly migration in relation to wind—the amassing of occurrence records—has deferred rather than brought nearer the discovery of the causal connexions involved (part I, p. 205).

That is not to say that we can expect to find no important differences between butterflies and locusts. For example, it seems that butterflies customarily retain more control than

locusts do over their own displacement, by more often avoiding flight in strong wind, keeping closer to the ground, and so on. During the southward migration of *Pieris brassicae* L. at Harpenden in 1940, which continued on every fine day for several weeks during which the wind blew from almost every quarter, Williams (1942) remarks that 'the only noticeable effect (of the wind) was that when it was strong a *few* butterflies seemed to be carried away with it against their inclination *and usually high in the air*' (my italics—J. S. K.):

'Nearly all butterflies when on migration tend to fly at the height which is normal for non-migratory flight, most individuals are below 10 feet, and few more than 20 feet above the ground, or above the tree tops if over forest land' (Williams 1949, p. 74).

Williams (*ibid.*) goes on to quote striking examples of the way butterflies regulate their height, moving up and down at a constant height over an uneven substrate.

The fact that butterflies keep closer control over their own displacement than do locusts, does not exclude the possibility of their migrations being directed *in the long run* by the wind. If closer control over their own displacement means less dependence of course and track upon the immediate wind, it also means there will be more chance of any given course, once set by an orientation reaction to the wind, or to any other agency, at a critical time such as at the start of migration in the morning, being maintained for hours afterwards when the migrants have ceased to orient to that agency (cp. p. 270). And the fact that butterflies have been seen flying equally often with and against the wind does not mean that they cover equal distances with and against the wind, i.e. that the two orientations are equally important in long-range migration. An example of short-range wind rectification, in Monarchs (*Danaus plexippus* L.), has been quoted on pp. 267–269. A more generally interesting example of wind rectification has been recorded for the Silver-Y moth, *Plusia gamma* L., in Denmark (Larsen 1949). The species sometimes migrates by day, when its directions do not show a regular relation to the wind direction (Williams 1949). But Larsen observed it migrating at night, when its displacement was consistently with the wind, the light (or rather the lack of light) perhaps rectifying the displacement down-wind (cp. p. 272).

If locusts exercise less control over their own displacement than do butterflies, the smaller, weak-flying insects such as aphids obviously exercise far less control than either locusts or butterflies. Aphids commonly rise to great heights, and their long-range movements are effected, in the narrowly mechanical sense, entirely by the wind (Fraenkel 1932; Glick 1939; Hardy & Milne 1938; Freeman 1945). But in what conditions of wind, temperature, light, etc., they take off and alight is governed by their own active behaviour (Davies 1935, 1936; Broadbent 1949). The main difference between them and the larger migrants is the relatively small contribution they make to their actual displacement over the ground. This difference is a merely quantitative one as far as behaviour is concerned, and provides no grounds for placing small insects like aphids in a separate behavioural category of passive migrants, distinct from a category of active or true migrants (cp. p. 279, and Kennedy 1950). In making their long migrations aphids require to be carried by the wind, but third, rectifying factors decide the direction, speed and extent of such movements by determining, through the insects' reactions, in what winds and for how long they fly.

There are other possibilities to be borne in mind which do not necessarily involve the wind. Lindroth (1948), for example, made observations which suggested a way in which

the long-range migrations of Carabid beetles might be directed by the sun through positive phototaxis. The mornings being too cold and day-times too windy, the beetles took off toward the sun mainly during warm, calm evenings and so flew westward, which is in accordance with the distributional evidence of their westward movement over the sea in spite of a prevailing south-westerly wind. In the terminology employed here, this westward trend would be ascribed to temperature and wind rectifying the primary directing influence of the sun. This example illustrates once again how the possibility of some environmental feature being responsible for the direction of a long-range movement cannot be dismissed simply because that feature's own direction varies.

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