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HIGH-ALTITUDE MIGRATION OF APHIDS IN MARITIME AND CONTINENTAL CLIMATES*

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INTRODUCTION

After taking samples of aphids regularly in the air over southern England for 3 years, Johnson (1951) wrote 'it is evident that there is a general tendency for aerial populations up to 2000 ft (610 m) to build up during the day and to decline at night, often leaving the air virtually clear of aphids in the early morning'. Reviewing the increasing evidence in 1965, Taylor still found 'All the evidence showed that, over southern England, the upper air cleared of aphids, and other insects, each night and a new aerial population built up each day'. Glick's (1939) catches, collected by aeroplane over Louisiana in the southern United States, remained anomalous, for he found 'more insects—at night, in proportion to the amount of time flown, than during the day'.

If insects continue to fly through the night, or resume flight on successive days as locusts do, they may migrate 1000 miles or more. Experimental evidence (Cockbain 1961a) suggests that few aphids will fly for long on the day after an exhausting full day's flight. Hence, the migratory ambit of an aphid species is probably limited by the ability of its individuals to fly through the night. Evidence from experiments suggests that night flight by aphids is unlikely, yet from circumstantial evidence of long-distance migration of the greenbug (*Schizaphis agrostis* Hille Ris Lambers = *Toxoptera graminum* Rondani) in the Central Plains of North America, overnight flight seems to be essential (Taylor 1965).

We therefore sampled aphids by day and night at 2000 ft (610 m) above ground over eastern Kansas, immediately in the path of the supposed migration, in low-level jet streams and compared aerial aphid densities directly with similar measurements made in earlier years over southern England.

The aphid community of the maritime aerial environment at high altitudes over England is thought to be maintained by aphids being constantly recirculated and constantly replenished by recruitment of new aphids from the ground, few remaining aloft for long and none overnight. If aphids are aloft over Kansas at night, this hypothesis needs to be modified, or extended to relate to the different, continental, aerial environment.

METHODS

The samples over southern England were collected by a suction trap at 1000 ft (305 m) above ground, suspended from a tethered balloon at Cardington, Bedfordshire (Johnson & Taylor 1955a, b) as part of a regular investigation of the aerial distribution of insects.

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The trap operated continuously, but only samples of aphids taken between 13.00 and 16.00 hours L.S.T. and between 01.00 and 04.00 hours on the next night are used for these comparisons. Catches were converted to aerial density from the tables in Taylor (1962a).

The samples over eastern Kansas were obtained with traps on aeroplanes, flying between Manhattan and Topeka at 2000 ft. A fine-mesh net (70 threads/in. = 27 threads/cm), supported by an outer stronger net, 21 in. (53.3 cm) in diameter, was suspended from a strut under each wing of a Cessna monoplane. The flights usually lasted about an hour between 13.00 and 16.00 hours, and again between 01.00 and 04.00 hours L.S.T. during the next night. The nets were exposed only during level flight at an airspeed of about 90 miles/h (145 km/h) and were assumed to be fully efficient (Taylor 1962b). The catches were converted to aerial density by relating them to the amount of air swept out by the nets on each flight.

Each complete sample unit consisted of a pair of estimates of aerial density, one in the mid-afternoon measuring current population density, and the other 12 h later assumed to be measuring the residual population left in the air after recruitment to the aerial population by take-off from terrestrial sources had ceased at nightfall. There are ten pairs of sample units from England and thirteen pairs from Kansas for analysis (Tables 1 and 2).

Table 1. *Aerial density per 10⁶ ft³ (10⁴ × 2.83 m³) of air of aphids between Manhattan and Topeka, Kansas, at 2000 ft (610 m)*

	13.00–17.00 hours			01.00–04.00 hours							
	Flying time (min)	Aphids caught	Density	Flying time (min)	Aphids caught	Density	Air temperature (°C)	Wind speed		Wind direction (degrees east of north)	
								miles/h	km/h		
1965											
July	7–8	57	2	0.92	112	0	0	21	17	(27.4)	80
	14–15	60	4	1.75	120	7	1.53	22	17	(27.4)	40
	22–23	60	1	0.44	120	0	0	30	29	(46.7)	200
	29–30	60	8	3.50	120	4	0.87	21	9	(14.5)	30
1966											
May	14–15	30	9	7.87	20	1	1.31	18	29	(46.7)	190
	19–20	29	12	10.85	58	1	0.45	18	18	(29.0)	250
June	3–4	60	3	1.31	57	3	1.38	18	35	(56.4)	180
	16–17	60	0	0	60	2	0.87	17	6	(9.7)	60
	23–24	58	2	0.90	60	0	0	23	29	(46.7)	170
	30–31	59	2	0.89	60	1	0.44	24	12	(19.3)	100
July	7–8	60	2	0.87	60	3	1.31	27	12	(19.3)	120
	21–22	60	16	6.99	61	4	1.72	23	18	(29.0)	120
	28–29	60	2	0.87	60	2	0.87	24	6	(9.7)	230
Σ		713	63		968	28					
Mean				2.86			0.82				

The aphids in the Kansas sample were identified to species so far as possible (Table 3). Air temperature, wind speed and direction at 2000 ft were interpolated from routine radio-sonde ascents at Topeka to correspond as closely as possible with sampling periods (Table 1). Night air temperatures at 1000 ft for the English sample were interpolated from routine radio-sonde ascents at Liverpool, Hemsby and Crawley (Table 2).

The two sets of samples differ in height, time and sampling technique. It is therefore

necessary to consider carefully the effects of these disparities between the methods and any resulting artifacts.

Table 2. *Aerial density, per 10⁶ ft³ (10⁴ × 2.83 m³) of air, of aphids at Cardington, England, at 1000 ft*

	13.00–17.00 hours			01.00–04.00 hours				
	Flying time (min)	Aphids caught	Density	Flying time (min)	Aphids caught	Density	Temperature (°C)	
1954								
June	17–18	15	1	16.00	180	0	0	14.5 ± 2.0
July	19–20	180	28	37.33	180	0	0	14.0 ± 1.0
	20–21	120	0	0	180	1	1.33	12.5 ± 1.0
	29–30	180	1	1.33	180	0	0	10.5 ± 0.5
August	3–4	180	11	14.67	180	1	1.33	16.0 ± 1.5
	26–27	180	5	6.67	180	0	0	14.0 ± 1.0
1955								
August	8–9	120	3	6.00	180	0	0	11.0 ± 1.0
	12–13	180	6	8.00	180	0	0	13.0 ± 0.5
	15–16	150	17	27.20	180	0	0	17.5 ± 0.5
	19–20	120	7	14.00	180	2	2.66	19.5 ± 2.0
Σ	1425	79			1800	4		
Mean			13.12				0.53	

Table 3. *Aphid species at 2000 ft (610 m) over Kansas*

	1965 and 1966						Total
	May		June		July		
	Day	Night	Day	Night	Day	Night	
Lachnidae	2	0	2	1	1	0	6
Callaphididae	5	0	0	0	0	0	5
<i>Rhopalosiphum maidis</i> (Fitch) [Corn leaf aphid]	0	0	3	3	30	19	55
<i>R. fitchii-padi</i> [Apple grain aphid]	0	0	1	0	0	0	1
<i>R. rufiabdominalis</i> (Sasaki)	0	0	0	0	1	0	1
<i>Schizaphis agrostis</i> Hille Ris Lambers = <i>Toxoptera graminum</i> (Rondani) [Green bug]	6	1	0	0	0	0	7
<i>Aphis</i> sp. <i>Sitobion avenae</i> (Fab.) = <i>Macrosiphum granarium</i> (Kirby) [English grain aphid]	0	0	0	1	0	0	1
Eriosomatidae	8	0	0	0	0	0	8
Other aphids	0	1	1	1	0	0	3
Other aphids	0	0	0	0	3	1	4
Total	21	2	7	6	35	20	91

English samples were collected at 1000 ft. Fig. 1 shows that the diurnal cycle of aerial density at 1000 ft hardly differs from that at 250 ft (76 m); the cycle at 2000 ft is more likely to be the same as at 1000 ft. We therefore assume the difference in sample heights over England and Kansas is irrelevant to the present issue.

Southern England was sampled in 1954–55 and eastern Kansas in 1965–66, but there is no reason to suppose the results were peculiar to any particular decade; the pressure systems at the two sites are different, so simultaneous sampling has no special value. The sampling months differed slightly, May–July in Kansas and June–August in England. Inspection of Table 1 shows no evident seasonal trends to invalidate the comparison.

Insects caught in suction traps can be retained inside the trap mechanism and released into a later sample, but these are usually so few that they can be ignored. However, in the present instance it is essential to consider the effect of even such small possible errors because the total sample is so small. The traps were changed in the morning, so that insects caught by day might be displaced into the night-time section of the catch and appear as night samples; the reverse could not happen. Hence an error would tend to diminish the difference between day and night catches. No such error was possible with the aeroplane samples. Any sampling artifacts would therefore tend to lessen, not emphasize, the distinction between the two sites.

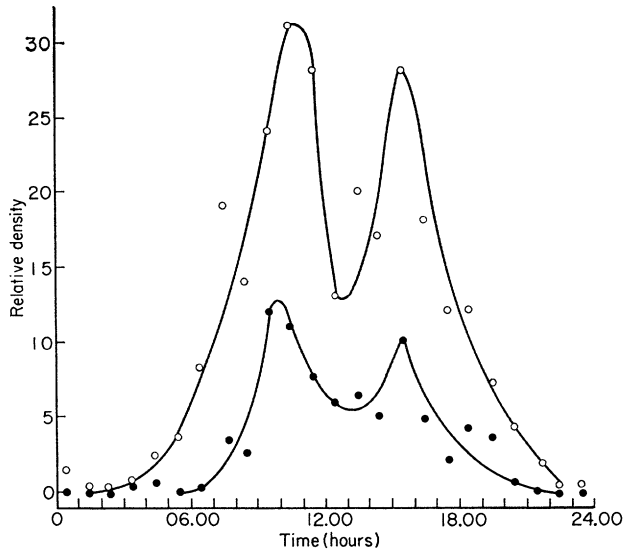


FIG. 1. Hourly changes in aerial aphid density at Cardington, southern England, August 1955. ○, 250 ft (76.2 m); ●, 1000 ft (305 m).

RESULTS

The nocturnal aerial density over Kansas averaged 34% of that during the preceding afternoon; over England it averaged 4%. Routine statistical tests for this kind of un-systematic and sparse data are not very satisfying. For example, the difference between the means of the proportions of night/day aerial densities, expressed as difference of logs

$$[\log (D_1 + 1) - \log (D_2 + 1)]/n$$

where D_1 is daytime density, D_2 is night density and n is the number of pairs of day-night samples at either site, gives $t = 2.87$ (d.f. 21) which is highly significant. However, there are many zeros and n is not large.

Again, summing the actual catches (Kansas sixty-three day, twenty-eight night; England seventy-nine day, four night) yields a highly significant χ^2 (17.8) in a 2×2 contingency test with Yates' correction, but this makes no allowance for differences between the sample size by day and night. Such differences are fortunately small and, if the appropriate small corrections are made to the catches, keeping the total catch constant, the proportions become sixty-eight/twenty-three (Kansas) and eighty/three

(England) and the distinction between the sites is further emphasized. χ^2 becomes 22.9 although the adjustment for sample size makes its validity suspect.

A more intensive treatment, by the maximum likelihood method, tests the hypothesis that β (England) \neq β (Kansas) where βN_i is the expected night catch and N_i' is the expected previous day catch corrected to standard sampling period. Catches n_i and n_i' , on day i and night i respectively, are obtained during flight periods t_i and t_i' respectively, and β is obtained by the iterative solution of the equations,

$$\beta = \frac{\Sigma n_i'}{\Sigma t_i' N_i} \quad : \quad N_i = \frac{n_i + n_i'}{t_i + \beta t_i'}$$

Analysis of χ^2 gives:

	β	χ^2	d.f.	P
England vs Kansas, difference of β	—	19.33	1	0.00001
England, consistency of β	0.042	14.87	9	0.10
Kansas, consistency of β	0.338	26.24	12	0.01

The results are quite conclusive; the proportion of night catch to day catch of aphids over England differed significantly from that over Kansas. The χ^2 analysis gives additional information. Over England the proportion, β , was not significantly different from one period to another in the few samples available, whereas, over Kansas, β differed significantly from one occasion to another. In other words, the inhibition of nocturnal flight over southern England was almost complete; over eastern Kansas, nocturnal flight occurred but additional factors affected the proportions remaining aloft, as might be expected.

Collectively these tests present a convincing argument for accepting the difference between the two sites as real, at least until further expensive experiments are done.

DISCUSSION

We have established that aphids were aloft over eastern Kansas at night, but not over southern England, confirming the difference between Glick's findings and Johnson's, and so far no simple component of the flight behaviour of aphids has been found to account for this (Halgren & Taylor 1968). It seems likely therefore that any explanation must be sought in the effect of the environment on the insects.

Three physical factors seem to limit high-altitude migration: temperature and light both limit take-off and flight, and atmospheric stability limits vertical movement. Within the restraints imposed by these factors, three kinds of horizontal movement are possible; inert drift, which may include gliding, active flights of short duration and enduring flights of many hours.

Temperature thresholds

The first essential for flight is adequate heat; the temperature threshold must be exceeded before take-off is possible. Few aphids take off at temperatures below 15° C; between 15 and 20° C some individuals of some species take off; above 20° C, temperature is less likely to inhibit take-off. Once the aphids are airborne, thresholds for continued flight are lower (Cockbain 1961b; Taylor 1963). Estimated night temperatures over Kansas usually exceeded 20° C; no nocturnal aphid flight was recorded at less than 17° C (Table 1). Over England, estimated night temperatures were usually below 15° C and only once

was 20° C possibly exceeded; half the aphids caught at night were on that one occasion (Table 2).

When aphids are dropped at temperatures below their flight threshold, they keep their wings closed and fall; Cockbain (1961b) and Halgren & Taylor (1968) used this response to investigate thresholds. Wellington (1945) wrote 'if . . . an insect is cooled below its minimum flight temperature, and folds its wings, as it invariably does, it will begin to fall. . . .' He does not, however, detail his evidence for this statement and there is, as yet, little information about how much cooling an aphid in active, lift-generating flight will tolerate before closing its wings.

Light thresholds

In laboratory tests, few aphids take off in light dimmer than 1 ft-candle (10.8 m-candles) (Dry & Taylor, unpublished). Light certainly fell below the take-off threshold by 02.00 hours both in England and Kansas; the light thresholds for continued flight are not well known. Neither is it known if such thresholds can be lowered during flight. Some Lepidoptera and Aleyrodidae, whose non-migratory flight is normally restricted to particular light intensities, fly continuously during day and night when migrating (Lewis & Taylor 1965). However, the aphids used in experiments on flight thresholds are presumed to be migrants and would be expected to have thresholds appropriate to migrants. There is no doubt that degrees of migratoriness exist in aphids (Shaw unpublished), so some aphids may be super-migrants, with thresholds lower than is normal for migrants.

Atmospheric stability

The daytime lift available to flying aphids comes from turbulent convection (Johnson & Penman 1951; Johnson 1957) and probably averages about 0.5 ft/sec (15 cm/sec). The air over southern England often clears of aphids for a short period in the early afternoon (see Fig. 1) although atmospheric lift does not diminish at this time. This suggests that the aphids are capable of escaping from atmospheric circulation and therefore are contributing significantly to their total lift, perhaps by supporting their own weight.

Aphids were caught at night over Kansas sometimes in low-level jet streams. Recruitment of aphids from ground level up to 2000 ft might then seem to be limited by the physical structure of these winds which are non-convective horizontal airstreams associated with inversions. Intense solar heating in middle-latitude continental plains, away from the moderating influence of oceans, produces strong turbulent convection that transmits the surface drag of wind near the ground upwards, restraining the wind velocity up to several thousand feet. This constraint ceases at sunset in clear weather when deep inversions break down eddy viscosity. The result is a wind that has a very stable velocity profile with a maximum, above the inversion, at about 03.00 hours at 2000–3000 ft, where it may exceed wind speeds near ground level by up to 70 miles/h (113 km/h), and has computed vertical velocities reaching only 0.07 ft/sec (2 cm/sec) (Blackadar 1957).

There may, however, be short periods of instability that cause strong gusts, lasting up to 30 min near the ground, and result in transfer of heat downwards in the inversion (Blackadar 1959). Low-level jets are also in some way associated with thunderstorms (Pitchford & London 1962), which again suggests associated instability. Therefore, during these periods of instability, lift which may exceed 0.07 ft/sec (2 cm/sec) is available.

In the Great Plains of North America jet streams are strongest from Oklahoma to Nebraska and their axes lie mainly between 170° and 225° east of north (Blackadar, personal communication). Such low-level jet streams cannot form in higher-latitude, maritime regions like Britain.

It has been suggested that low-level jet streams provide special conditions inducing night flight of aphids, as distinct from providing a vehicle for aphids already in flight. Our results do not confirm this. When the nocturnal density of aphids over Kansas, as a proportion of the preceding daytime density, is plotted against the direction of the nocturnal winds, there is no correlation with the predominantly south-north trajectory of the jet streams (Fig. 2), neither is there any significant correlation with wind speed (Table 1).

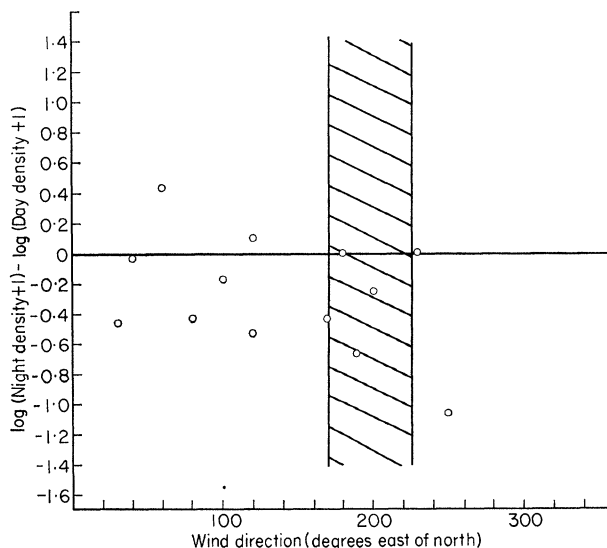


FIG. 2. Ratio of night/day aerial aphid densities at 2000 ft (610 m) at Manhattan, eastern Kansas, in relation to wind direction. Shaded area, prevailing axes of low-level jet streams.

Inert drift

Pringle (1957, p. 25) suggested that aphids can hold their wings extended without movement and this 'habit . . . may assist in their dispersal by air currents in the atmosphere'. Terminal velocities of falling anaesthetized aphids were measured and found to be:

- | | |
|--|-------------------------|
| (1) <i>Toxoptera graminum</i> | 3.3 ft/sec (101 cm/sec) |
| (2) <i>Rhopalosiphum maidis</i> (Fitch) | 4.5 ft/sec (137 cm/sec) |
| (3) <i>Aphis fabae</i> Scop. | 5.3 ft/sec (162 cm/sec) |
| (4) <i>Acyrtosiphon pisum</i> (Kaltenbach) | 6.3 ft/sec (192 cm/sec) |

The differences depended on the size of the species and not whether the wings were open or closed. This agrees with Wellington's (1945) findings that 'the more minute insects require vertical currents of the same magnitude to support them, whether the wings are extended or folded'. Thus, extended wings do not assist aphids to disperse unless they also flap, or can be flexed to promote true gliding. Even the small aphids, therefore, require atmospheric lift of about 3 ft/sec (91.4 cm/sec) to remain airborne without flight, whether their wings are open or closed. Lacking this lift, aphids must fly

or fall, and, because nearly all aphids are below 10 000 ft (3048 m) the air will then clear of aphids in less than 1 h, irrespective of the speed of the horizontal element of the wind which contributes nothing to lift except in true gliding flight. True gliding has not been found in aphids.

Flight times

In *Aphis fabae* and *Myzus persicae*, 2 h initial flight usually induces settling (Cockbain, Gibbs & Heathcote 1963) and continuous free flights by *Aphis fabae* rarely exceed 3 h in flight chambers (Kennedy & Booth 1963). By relating daytime bimodal flight periodicity at high altitudes, as in Fig. 2, to take-off periodicity at ground level, daytime flights have been estimated to last less than 4 h over southern England (Johnson 1957; Taylor 1958).

CONCLUSIONS

Inert drift of aphids for long distance at night is probably insignificant because vertical wind velocities greater than 3 ft/sec (91 cm/sec) are unlikely; even during daytime such upcurrents are local.

By individual aphids making short flights of less than 4 h, they could maintain the measured aerial densities over England, because by day the population is constantly replenished and at night the population disappears. Many aphids fly at night over Kansas; therefore individuals must fly longer, because although nocturnal Kansas temperatures would permit take-off to replenish the aerial population, light would not. Nocturnal flights over Kansas must therefore last longer than 6 h, at least from nightfall to 02.00 hours. Small-scale turbulence probably produces some vertical movement at night, but, with the breakdown of large-scale convection cells at sunset, aphids may not be brought down near enough to the ground for landing to be possible (Taylor 1960). Aphids in daytime flight over England are lifted to high altitudes and subsequently brought back to ground almost entirely by atmospheric circulation; the short time spent by aphids at a high altitude over England is therefore largely imposed upon them by atmospheric circulation. This also seems to happen with other insects such as *Oscinella frit* L. which also spends only short periods at high levels (Johnson, Taylor & Southwood 1962) although, unlike aphids, it can fly intermittently for many days (Rygg 1966).

We therefore suppose that, having taken off in the brighter light of day, many aphids keep flying when light intensities diminish at night so long as the air is warm enough, as it is over Kansas. But should the atmosphere clear of aphids at night, dim light will prevent take-off and thus its repopulation; in England cold at night also usually inhibits take-off. During the long twilight over England, slowly subsiding atmospheric circulation may gradually bring down the aphids before inversions form. The quicker change from day to night in the lower Kansas latitudes perhaps leaves aphids at high altitudes cut off, by rapidly formed inversions, from the circulation necessary to bring them down, until darkness breaks visual contact with the ground and flight continues, for lack of alighting stimuli, in what is almost a sensory vacuum.

Springtime aeroplane flights over Kansas might show whether jet streams carry aphids at ambient temperatures below their flight threshold when they can contribute no lift to maintain height. However, fewer aphids are then in flight and adequate samples more difficult to obtain. The complementary experiment, to find whether aphids fly overnight over England when ambient temperatures aloft exceed the flight threshold, is hindered by the rarity of such occasions. Nevertheless, out of four aphids caught over England at

night in the samples discussed here, two occurred on the one occasion when ambient temperature approached 20° C.

Taylor (1965) listed four possible modes of aphid migration: directed boundary layer flight, stratiform drift, cumuliform dispersion and jet stream transport. Of these only the last was thought to permit nocturnal movement of aphids; the evidence presented here shows that aphids do fly at night in jet streams, but they also fly when no jet stream is flowing; examination of the number and behaviour of other insects in flight at night might show how much this nocturnal migration owes to flight behaviour peculiar to aphids.

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SUMMARY

1. Aphids were sampled at 2000 ft (610 m) above ground over eastern Kansas, U.S.A. and at 1000 ft (305 m) above ground over southern England in summer.

2. Afternoon aerial densities were higher over southern England, but night-time densities much lower, than over Kansas.

3. A significantly larger proportion remained aloft overnight over eastern Kansas and the difference is not attributable to sampling artifacts.

4. Night air temperatures were predominantly above the flight threshold over eastern Kansas and below it over southern England.

5. The low-level jet stream over eastern Kansas may be transporting actively flying aphids, but it was not responsible for the high overnight aerial densities.

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