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LIGHT AND TEMPERATURE THRESHOLDS FOR TAKE-OFF BY APHIDS

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INTRODUCTION

Migratory flights by aphids can begin only when weather, especially light and temperature, permits take-off. For example light and temperature thresholds for take-off restrict the flight of *Aphis fabae* leaving its host plant within the daylight hours (Johnson & Taylor 1957). Once airborne, the temperature thresholds for continued flight differ considerably from those for take-off (Cockbain 1961; Taylor 1963).

Some species of aphid, notably *Schizaphis graminum*, have been repeatedly recorded as migrating long distances. Because of the time taken for such migration, aphids must fly for more than one period of daylight and several species, including *S. graminum*, have been sampled at 2000 ft (609 m) over Kansas during the night (Berry & Taylor 1968).

Hence either flight must continue, or take-off occur, during the night when light and temperature are most likely to be limiting (Taylor 1965). There is little evidence about continued flight at very low light intensities (Halgren & Taylor 1968); we here consider whether nocturnal take-off can contribute to overnight flights.

We measured light and temperature thresholds for take-off by several species of aphid, including *Aphis fabae* and *Schizaphis graminum*, to seek specific limiting values that may permit, or prevent, nocturnal take-off as a prelude to long distance migration. The experiments showed also that some alatae were unwilling to take flight a second time, no matter how short the first flight had been and that some did not take off, as expected, at the end of the teneral period (Taylor 1957). This complicates the presentation of the temperature thresholds and has led to a revision of the former view of migrant aphids discussed elsewhere (Shaw 1968a, b).

MATERIALS AND METHODS

The aphids

Rhopalosiphum maidis (Fitch) the corn-leaf aphid

Biotypes KS-1 (Cartier & Painter 1956)	Expts 1, 9.
KS-2 (Cartier & Painter 1956)	Expts 2, 10, 11.
KS-3 (Painter & Pathak 1962)	Expts 3, 12.
KS-4 (Painter & Pathak 1962)	Expts 4, 13.

KS-1 and KS-2 were clones from single individuals of the cultures originated by Cartier & Painter (1956) and maintained by the Department of Entomology, Kansas State University. Similarly KS-3 and KS-4 were clones from single individuals of the cultures originated by Painter & Pathak (1962); it is uncertain whether the cultures had remained unchanged since they were established.

Schizaphis (= *Toxoptera*) *agrostis* (= *graminum*) Hille Ris Lambers, the greenbug: Expts 5, 14, 15, 16, 17.

'Laboratory strain' was a clone taken from a long-established mixed culture maintained by the Department of Entomology, Kansas State University.

'Field strain' was a mixed culture from about twenty individuals collected from volunteer wheat at Bushland, Texas, by N. E. Daniels in December 1964, i.e. immediately before use.

Macrosiphum granarium Kirby (= *Sitobium avenae* Fab.), the English grain aphid: Expts 6, 18.

Rhopalosiphum fitchii (Sanderson), the apple grain aphid: Expts 7, 19.

Acyrtosiphum pisum (Harris), the pea aphid: Expts 8, 20, 21.

These three species were clones derived from established cultures maintained at Kansas State University.

Aphis (= *Doralis*) *fabae* Scop., the black bean aphid: Expt 22. This was from a clonal culture maintained by the Department of Entomology, Rothamsted Experimental Station (Taylor 1957; Cockbain 1961).

Pea and bean aphids were cultured on broad bean (*Vicia faba*) and cereal aphids on barley varieties Reno and Missouri in pots in 18 × 18 × 20 in. (45.7 × 45.7 × 50.8 cm) glass and gauze cages, in a glasshouse at temperatures from 24 to 28° C, humidity 40–70%, with day-length extended to 18 h by incandescent electric light.

Individual aphids were kept on a bean plant in a pot, or on a barley leaf in water, under 5 × 1¼ in. (12.7 × 3.2 cm) cellulose acetate and gauze cages, before use.

Procedure

Preliminary tests showed that *Rhopalosiphum maidis*, *Macrosiphum granarium* and *Rhopalosiphum fitchii*, collected after their first brief flight to the top of the breeding cage, did not fly a second time from their host plants, cereals. After collection from the cage top, they were therefore kept on separate bean plants before use (Expts 1, 2, 3, 4, 6, 7, 9, 10, 12, 13, 18, 19). Many *Schizaphis graminum* and *Acyrtosiphum pisum* would not take off a second time from an unsuitable host. These species were therefore transferred as fourth instar alate nymphs to separate host plants and kept until flight-mature before they were used on their first flight (Expts 5, 8, 14, 15, 20); *Aphis fabae* was treated likewise (Expt 22).

Schizaphis graminum collected from the top of the culture cage (Expt 16) did, however, take off a second time when kept at 10° C for 4 days on bean plants. When taking off from glass, *Rhopalosiphum maidis* KS-2 (Expt 11), *Schizaphis graminum* (Expt 17) and *Acyrtosiphum pisum* (Expt 21) were collected from the top of the culture cage and kept for 15 min in a glass beaker at 10° C in the dark, before use. These aphids were therefore taking off for the second time.

Experiments were done in a Percival E-57 Environator. While the other variable was held constant, temperature, or light, was gradually increased and was recorded as each aphid took flight, giving results in the form of a frequency distribution.

Light thresholds

Light was provided by various combinations of lamps with no attempt to control wavelength; intensity at plant level was measured by Weston Illumination Meter Model 756 (Table 1).

Rhopalosiphum maidis, *Macrosiphum granarium* and *Rhopalosiphum fitchii* were kept

on bean plants at 20° C, in darkness for 30 min, then at the test temperature for 15 min before being exposed to the dimmest light (Expts 1, 2, 3, 4, 6, 7). *Schizaphis graminum* and *Acyrtosiphum pisum* were retained on individual host plants in the dark at the test temperature until flight-mature (Expts 5, 8). Experiments were done at night, under a black hood to exclude extraneous light.

The aphids were exposed in batches to each progressively increased light intensity for 5 min and the take-offs counted. Batches were accumulated until at least 100 individuals had taken flight. During the tests, temperatures were held constant at 26° C for *Rhopalosiphum fitchii*, 30° C for *Macrosiphum granarium*, *Rhopalosiphum maidis* and *Acyrtosiphum pisum* and 40° C for *Schizaphis graminum*; these temperatures were necessary to ensure that cold did not inhibit flight, as found in the temperature experiments.

Table 1. *Experimental light values*

Source	Light at plant surface	
	ft-candles	m-candles
Six night lights	0.125	1.35
7 W incandescent, shielded	1.5	16.2
7 W incandescent	3.5	37.8
40 W incandescent	11.0	118.8
75 W incandescent (high)	24.0	259.0
75 W incandescent (low)	40.0	432.0
All incandescents	80.0	864.0
2 × 80 W fluorescents	120.0	1296.0
4 × 80 W fluorescents	240.0	2392.0
8 × 80 W fluorescents	560.0	6048.0
All available lamps	630.0	6804.0

All light measurements made with Weston Illumination Meter No. 756.

Temperature thresholds

Experiments were done in the morning. *Rhopalosiphum maidis*, *Macrosiphum granarium* and *Rhopalosiphum fitchii* were held at 10° C overnight before use (Expts 9, 10, 12, 13, 18, 19). *Schizaphis graminum*, *Acyrtosiphum pisum* and *Aphis fabae* taking off from host plants were kept for at least 15 h at 25° C in the dark to become flight-mature before use (Expts 14, 15, 20, 22).

Batches of suitable aphids were exposed to full daylight at an initial temperature about 12° C which was then increased gradually to about 40° C during 2–3 h. The take-offs were counted at 1° C intervals and counts for batches of aphids were accumulated until at least 100 individuals had taken flight.

Additional experiments were done on once-flown *Rhopalosiphum maidis* KS-2, *Schizaphis graminum* and *Acyrtosiphum pisum* taking off from a glass surface (Expts 11, 17, 21), and on *Schizaphis graminum* taking off from beans after 4 days at 10° C in the dark (Expt 16).

RESULTS

Light thresholds

The possible range of light intensities was limited, 0.125–630 ft-candles (1.35–6804 m-candles) (Table 1), but seemingly adequate because only *Schizaphis graminum* and *Rhopalosiphum maidis* KS-1 took flight in appreciable numbers in the brightest light

Table 2. Take-off in relation to light—the total number of aphids, from repeated trials, that took flight as light increased in steps from 0-125 to 630 ft-candles

Expt no.	Species	Strain or biotype	Surface	light (ft-candles)												Total take-off	Total did not take-off
				log light	1-10	1-125	1-5	3-5	11-0	24-0	40-0	80-0	120-0	240-0	560-0		
1	<i>Rhopalosiphum maidis</i>	KS-1	Bean	1	3	10	6	7	13	20	19	13	14	15	121	42	
2	<i>R. maidis</i>	KS-2	Bean	5	7	4	14	15	16	10	16	8	6	0	101	18	
3	<i>R. maidis</i>	KS-3	Bean	1	2	8	13	12	19	22	20	14	12	7	130	24	
4	<i>R. maidis</i>	KS-4	Bean	0	4	8	7	8	11	20	20	20	21	9	128	40	
5	<i>Schizaphis graminum</i>	Lab. strain	Barley	3	4	4	4	8	8	11	14	17	14	16	103	29	
6	<i>Macrosiphum granarium</i>	Lab. strain	Bean	7	15	18	25	28	23	21	8	6	1	0	152	10	
7	<i>Rhopalosiphum fitchii</i>	Lab. strain	Bean	1	1	2	6	11	39	35	40	31	13	7	186	23	
8	<i>Acyrtosiphum pisum</i>	Lab. strain	Bean	3	2	8	22	25	24	23	11	14	12	5	149	17	

(Table 2). Cumulative percentage probabilities of take-off against log light intensity are all slightly skewed. Adding a constant (c) to light intensity before taking logs gives linear responses (Fig. 1), except that the response of some species falls rapidly towards zero as light closely approaches the value c . In other words, in the regression equation

$$y = a + b \log(x + c)$$

where y = percent probability of take-off; x = light intensity in ft-candles (m-candles); a = intercept when light = 0 ft-candles (m-candles); b = regression coefficient; and

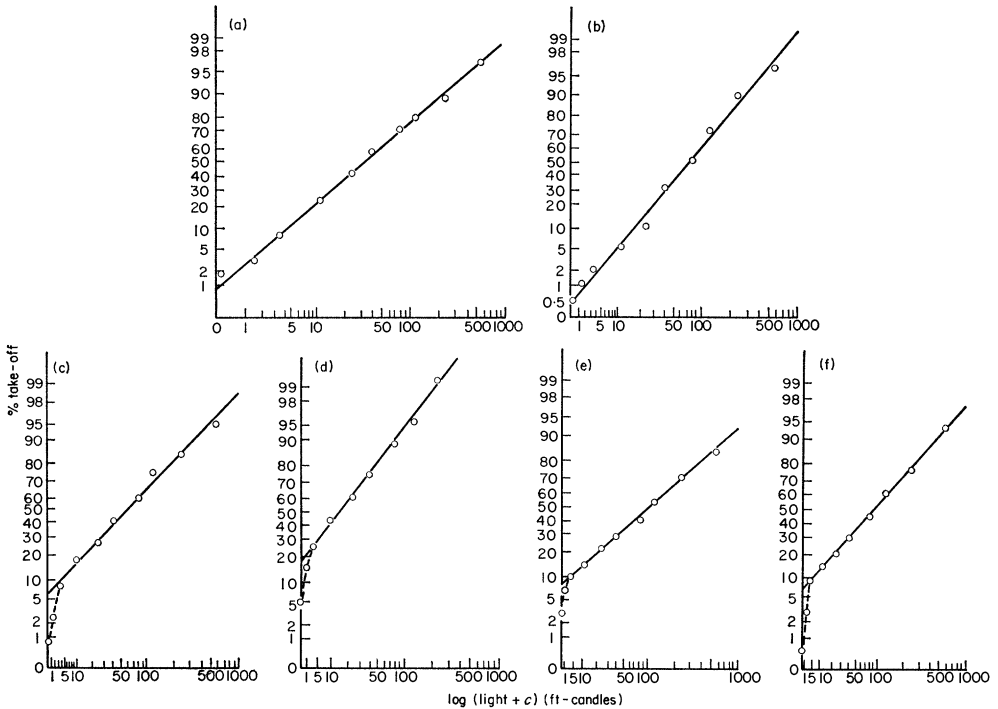


FIG. 1. Percentage probability of aphid take-off in response to $\log(\text{light} + c)$ where c varies from 1 to 20 ft-candles (10.8–216 m-candles) according to species. (a) *Acyrtosiphum pisum*; (b) *Rhopalosiphum fitchii*; (c) *R. maidis* KS-3; (d) *Macrosiphum granarium*; (e) *Schizaphis graminum*; (f) *Rhopalosiphum maidis* KS-4. There is often a discontinuity in very dim light. The remaining two response curves for KS-2 and KS-1 are very like *Macrosiphum granarium* and *Schizaphis graminum* respectively.

c = added constant before taking logs, the intercept value (a) does *not* imply take-off in the dark.

Table 3 gives the regression constants, fitted by eye because the observations are too few for iterative fittings of so many constants. The 5% take-off value (Table 3) is estimated by eye from the tail of the curve and the 50% and 95% values read from the straight line. The value of the added constant (c) ranges from 1 to 20 ft-candles (10.8 to 216 m-candles), the regression coefficient (b) from 0.84 to 1.33 and the intercept (a) from 0.5 to 18% but these constants seem not to be intercorrelated. However, the 5, 50 and 95% values for the species and biotypes form recognizable groups. *R. maidis* KS-2 and *Macrosiphum granarium* responded to the dimmest light, 5% taking off at 0.1 ft-candles (1.08 m-candles) and 95% at 110–200 ft-candles (1188–2160 m-candles) with the median (50%) at 15–28 ft-candles

(162–302.4 m-candles). *Acyrtosiphum pisum*, *Rhopalosiphum fitchii* and *R. maidis* KS-3 responded between 2–9 ft-candles (21.6–97.2 m-candles) (5%) and 415–520 ft-candles (4482–5616 m-candles) (95%) with medians at 35–71 ft-candles (378–767 m-candles). Close to these in response range were *R. maidis* KS-1 and KS-4 ranging from 2 ft-candles (21.6 m-candles) (5%) to 680–860 ft-candles (7344–9288 m-candles) (95%) with medians at 80–85 ft-candles (864–918 m-candles), although their distributions were more strongly skew ($c = 15–20$). *Schizaphis graminum* had the widest range of all with the 5% limit fairly low (1 ft-candle : 10.8 m-candles), the extrapolated 95% limit very high (1350 ft-candles : 14580 m-candles), and the median at 100 ft-candles (1080 m-candles). Only in *Rhopalosiphum maidis* KS-2 and *Macrosiphum granarium* did small proportions of the population take flight in light as dim as civil twilight. All species required light

Table 3. Percentage probability of response = $a + b \log(\text{light} + c)$

Expt no.		c (ft-candles)	b	a (%)	5%	50%	95%
8	<i>Acyrtosiphum pisum</i>	1	0.84	1	2	35	420
7	<i>Rhopalosiphum fitchii</i>	5	1.23	0.5	9	71	415
3	<i>R. maidis</i> KS-3	10	1.04	6*	2	60	520
2	<i>R. maidis</i> KS-2	10	1.23	10*	0.1	28	200
6	<i>Macrosiphum granarium</i>	10	1.33	17*	0.1	15	110
5	<i>Schizaphis graminum</i>	15	0.84	8.5*	1	100	1350
1	<i>Rhopalosiphum maidis</i> KS-1	15	0.93	9*	2	80	860
4	<i>R. maidis</i> KS-4	20	1.11	18*	2	85	680

* Cut off at low light.

Species constants derived from the regression equation $y = a + b \log(x + c)$, where y = percentage probability of take-off and x = light intensity in ft-candles, fitted graphically as in Fig. 1.

about equivalent to sunrise or sunset for 50% take-off and *Schizaphis graminum* required light equivalent to full sunlight for 95% of the population to take flight, i.e. more light than the honey bee for maximum visual acuity (Hecht & Wolf 1929). There is no likelihood of these aphids continuing to take off from either host or non-host plants during the night, even when it is hot.

Temperature thresholds

The temperature thresholds are unexpectedly high and, because some aphids were unwilling to fly, are suspect. In these experiments no aphid took flight below 14° C and most required 20–30° C for take-off; some even required 40° C. Aphids of the same species from cultures raised under other conditions would certainly have lower thresholds; *Aphis fabae*, for example, took off from beans at temperatures between 16 and 31° C compared with 16–20° C at Rothamsted. *Schizaphis graminum* continued to take off from barley at temperatures up to 41° (Table 4). Nor were the response curves simple. Most response curves were best fitted by double normal distributions for which the means, standard deviations and areas are given in Table 5. These distributions were fitted by computer using a program, written by K. E. Bicknell, to the model

$$\hat{y}_j = \sum_{i=1}^{i=n} \frac{F_i}{s_i \sqrt{2\pi}} \cdot \exp \left[\frac{-(x_j - \mu_i)^2}{2s_i^2} \right]$$

where y_j is the calculated value corresponding to the j th observation, x_j is the j th value of x , n is the number of component distributions, F_i is the i th scaling factor, μ_i is the i th mean and s_i is the i th standard deviation.

Table 5. Temperature thresholds expressed as single or double normal thresholds*

Expt no.	Aphid species	Biotype or culture	Take-off surface	Flight no.	Take-off temperatures Medians \pm S.D.			Take-off categories (% of population in each fraction)			
					Lower	Single	Upper	Lower	Upper	Non-flyers	
9	<i>Rhopalosiphum maidis</i>	KS-1	Bean	2		26.4 \pm 2.62			54.2		45.8
10	<i>R. maidis</i>	KS-2	Bean	2		25.1 \pm 1.82			64.4		35.6
11	<i>R. maidis</i>	KS-2	Glass	2		20.5 \pm 1.54			98.3		1.7
12	<i>R. maidis</i>	KS-3	Bean	2		27.0 \pm 2.60			57.9		42.1
13	<i>R. maidis</i>	KS-4	Bean	2		23.4 \pm 1.22		27.1 \pm 1.37		28.1	60.1
14	<i>Schizaphis graminum</i>	Field	Barley	1		27.8 \pm 5.12		38.0 \pm 1.32	16.4	81.7	1.9
15	<i>S. graminum</i>	Lab.	Barley	1		28.5 \pm 1.28		37.9 \pm 2.45	10.9	84.4	1.9
16	<i>S. graminum</i>	Lab.	Bean (4 days)	2		23.1 \pm 2.41		27.8 \pm 1.05	71.0	19.3	9.7
17	<i>S. graminum</i>	Lab.	Glass	2		25.8 \pm 2.47		32.6 \pm 1.14	66.5	27.1	6.4
18	<i>Macrosiphum granarium</i>	Lab.	Bean	2		18.8 \pm 1.83		23.2 \pm 3.38	66.9	30.1	3.0
19	<i>Rhopalosiphum ficthii</i>	Lab.	Bean	2		23.9 \pm 3.30			78.3		21.7
20	<i>Acyrtosiphum pisum</i>	Lab.	Bean	1		20.2 \pm 2.27		28.0 \pm 3.16	42.9	29.8	27.3
21	<i>A. pisum</i>	Lab.	Glass	2		21.8 \pm 0.80		26.7 \pm 2.09	21.2	65.0	13.8
22	<i>Aphis fabae</i>	Lab.	Bean	1		21.1 \pm 2.25		28.6 \pm 1.99	52.8	23.9	23.3

* The measurements were made in 1° C intervals, hence the mean for distributions is 0.5° C less than the medians for thresholds given here.

'Laboratory' and 'field' cultures of *S. graminum* did not differ apparently, so it seems improbable that these responses resulted from the prolonged culture of some of the aphids.

DISCUSSION

As expected (Taylor 1963), individual aphids had a threshold response to both light and temperature which appears as a probability distribution in a population, and not as a continuum such as is suitable for untransformed regression analysis. For all species, temperature below 14° C inhibited take-off completely and for most species temperatures exceeding 31° C produced no further response. Response to log light intensity was uni-modal, not normal, and with a cut-off in dim light (Fig. 1). Otherwise the light response

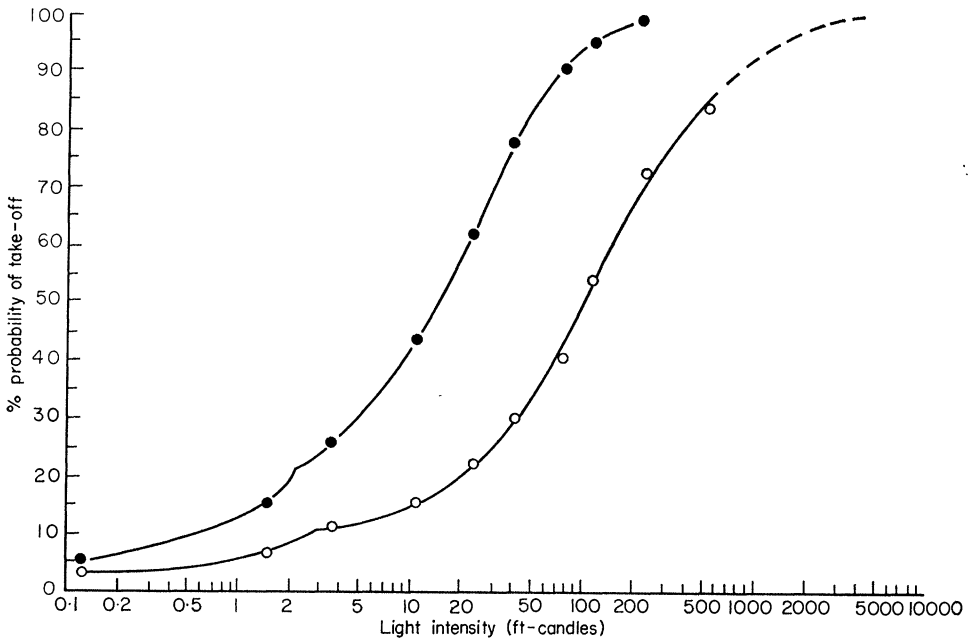


FIG. 2. Light response thresholds for take-off by *Macrosiphum granarium* (●) and *Schizaphis graminum* (○); thresholds for other species fell between these extremes.

was as expected and with only one species, *Schizaphis graminum*, was additional take-off implied in light above 1000 ft-candles (10800 m-candles) (Fig. 2).

Thus the light reaction seems less susceptible than the temperature reaction to other environmental variables, presumably culture conditions.

The most profound difference from previously reported take-off behaviour was the evident unwillingness of some aphids to take flight in these experiments. It was the drive to leave even an apparently desirable host that had previously allowed the teneral period to be defined as the developmental interval between eclosion and flight (Taylor 1957). It now seems that the earlier field experiments on *Aphis fabae* in southern England (Johnson, Taylor & Haine 1957) and the subsequent laboratory experiments using culture conditions similar to those in the field (Johnson & Taylor 1957; Taylor 1957) were, by chance, those conditions most conducive to the production of fully migrant alate *A. fabae*. For example, in one set of those teneral experiments only eight alatae out of a total of

194 alate nymphs failed to take flight. Of these, four were recorded as 'damaged', three as 'reproducing' and one 'will not fly'. At that time those insects were discarded as being probably damaged; it remains probable that some were damaged and that those culture conditions produced more than 95% migrants amongst alatae.

In the present series of experiments *A. fabae* was included after the other five species had shown various degrees of unwillingness to fly, thus making the measurement of teneral time on the old criterion impossible. The original clonal culture of *A. fabae* from

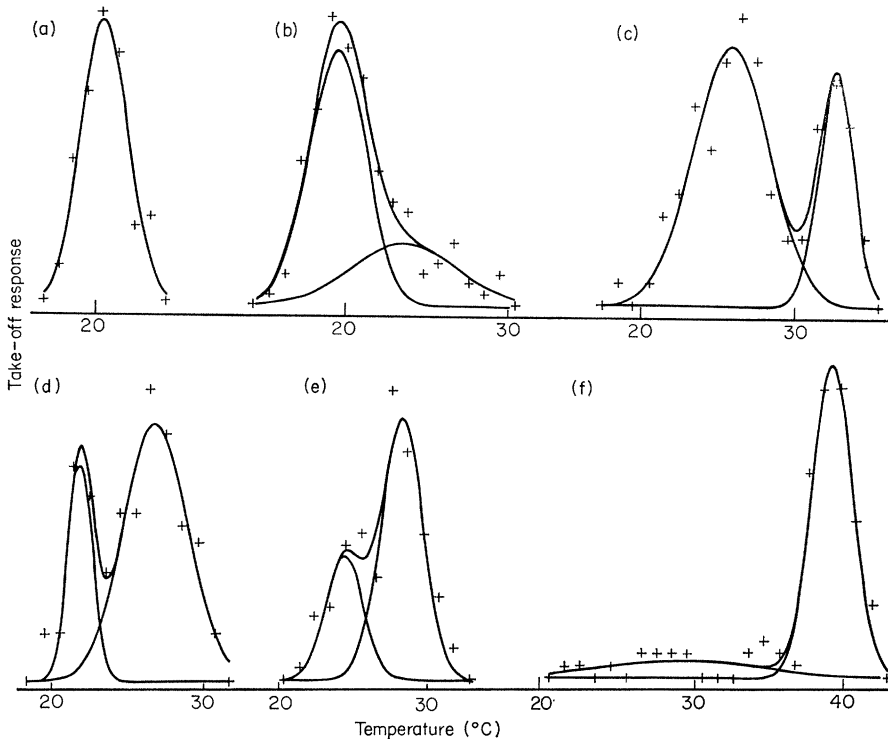


FIG. 3. Temperature response curves were sometimes unimodal and sometimes bimodal. All were fitted with one or two normal distributions. (a) *Rhopalosiphum maidis* KS-2 on glass; (b) *Macrosiphum granarium* on bean; (c) *Schizaphis graminum* on glass; (d) *Acyrthosiphum pisum* on glass; (e) *Rhopalosiphum maidis* KS-4 on bean; (f) *Schizaphis graminum* on barley (field strain). The vertical scale is adjusted for each figure to equalize the maximum response; data in Table 3.

Rothamsted was then found to be unwilling to fly when cultured at Manhattan. The main difference was in the high temperature in the glasshouse at Manhattan which affected not only the aphids but also the plants to an unknown extent. It is not suggested that the effect was solely a direct one on the aphid; it may also have acted through colony structure, nutrition or water balance. However, migratoriness is evidently not a necessary concomitant of alateness in aphids.

The two parts of the curve of response to temperature, especially by *Schizaphis graminum* taking off from barley (Fig. 3), may be interpreted as the response of two physiologically different fractions of the population. The aphids that take off at high temperatures may be unwilling migrants, anatomically able to fly but induced to migrate only by immediate

environmental pressure, in contrast to those aphids that migrate at the end of the teneral period and for whom migration is an evolved requirement before reproduction can begin. In our experiments heat approaching the upper thermal tolerance limit seems to have provided the extra stimulus needed. In experiments of this kind an aphid usually remains feeding quietly until the temperature rises to a certain level when it walks rapidly to the top of the leaf, waves its antennae, folds and unfolds its wings, raises its head and lowers its abdomen, then takes flight. Many taking off at high temperatures seemed agitated, their movements lacked coordination and some fell in attempting to take flight.

When *S. graminum* was placed on a non-host, beans or on glass, many took off at lower temperatures than from barley. This did not happen with *Acyrtosiphum pisum* (Table 5). In addition to the two fractions of the aphid population that took off at different temperature ranges, there is a third fraction that failed to fly at all in these experiments. However, the proportion in each segment is not explained simply in terms of substrate and temperature. In addition, some of the *Schizaphis graminum*, *Acyrtosiphum pisum* and *Aphis fabae* were taking flight for the first time, whereas *Rhopalosiphum fitchii*, some *R. maidis* and *Macrosiphum granarium*, were taking their second flight; hence some aphids may have been inadvertently rejected because only those individuals that took flight at the first opportunity were used in the experiments. Some aphids reproduced before take-off; for example, of fifty plants examined from which *Aphis fabae* had flown, twenty-two carried a total of forty-eight nymphs. These experiments were not designed to investigate differences in 'willingness' to fly, or migratoriness within species. Small differences in culture techniques between species may have altered the proportion of those aphids that responded at different temperature thresholds. No explanation of the proportions that behaved differently is therefore offered. However, there is obviously a range of flight 'willingness' in most, or all, of these species that is affected by both their physical environment and their substrate. In the light threshold experiments, both the temperature and the 'willingness' effects were eliminated by using very high temperatures and no further interaction with light was apparent; except that some individuals failed to fly, the response curves were as expected.

Although the temperature thresholds for take-off that we found probably did not represent those in the field, except perhaps in very hot climates, there seems no reason to doubt the general validity of the light thresholds. That aerial populations are replenished by individuals taking off from the ground during the night is thus improbable, so it must be concluded that, when long-distance migration can be explained only by continuous flight for more than one daytime period, the aphids must have taken flight during the preceding daytime and flown throughout the night.

The proportion of aphids (5–10%) that in near darkness respond to falling by active flight (Halgren & Taylor 1968) is probably too small to account for the nocturnal aerial population found by Berry & Taylor (1968). We therefore conclude that an aphid already in flight will continue to fly as the light diminishes down to light intensities that fail to evoke either a falling aphid to fly or a settled one to take off.

ACKNOWLEDGMENTS

We are grateful to K. E. Bicknell of the Computer Department, Rothamsted, who wrote the curve-fitting program. The second author held a Senior Foreign Scientist Fellowship supported by the National Science Foundation while a Visiting Professor at Kansas

State University. The first author used a portion of the work reported here, in partial fulfilment of the requirement for a Ph.D. in Entomology (Dry 1965).

SUMMARY

(1) Median take-off thresholds for light intensity of eight lines of five species of alate alienicolae aphids were between 15 and 100 ft-candles (162–1080 m-candles).

(2) Distributions were skew and corrected by adding a constant, between 1 and 20 ft-candles, to light intensity before taking logs.

(3) Small proportions of the population of *Rhopalosiphum maidis* KS-2 and *Macrosiphum granarium* responded to light equivalent to civil twilight (0.1 ft-candle : 1.05 m-candles).

(4) *Schizaphis graminum* required the brightest light (1350 ft-candles : 14580 m-candles) for full response.

(5) These aphids are unlikely to take flight at night.

(6) Temperature thresholds were unexpectedly high and complex.

(7) No aphids took flight below 14° C.

(8) Some aphids flew only at temperatures near the upper tolerance limit.

(9) Migratory flight is not a necessary concomitant of the alate condition in these aphids.

REFERENCES

- Berry, R. E. & Taylor, L. R. (1968). High-altitude migration of aphids in maritime and continental climates. *J. Anim. Ecol.* **37**, 713–22.
- Cartier, J. J. & Painter, R. H. (1956). Differential reactions of two biotypes of the corn leaf aphid to resistant and susceptible varieties, hybrids and selections of sorghums. *J. econ. Ent.* **49**, 498–508.
- Cockbain, A. J. (1961). Low temperature thresholds for flight in *Aphis fabae* Scop. *Entomologia exp. appl.* **4**, 211–9.
- Dry, W. W. (1965). *Teneral periods, take-off and flight thresholds of selected species of Aphididae*. Unpublished Ph.D. dissertation, Kansas State University.
- Halgren, L. A. & Taylor, L. R. (1968). Factors affecting flight responses of alienicolae of *Aphis fabae* Scop. and *Schizaphis graminum* Rondani (Homoptera : Aphididae). *J. Anim. Ecol.* **37**, 583–93.
- Hecht, S. & Wolf, E. (1929). The visual acuity of the honey bee. *J. gen. Physiol.* **12**, 727–60.
- Johnson, C. G. & Taylor, L. R. (1957). Periodism and energy summation with special reference to flight rhythms in aphids. *J. exp. Biol.* **34**, 209–21.
- Johnson, C. G., Taylor, L. R. & Haine, E. (1957). The analysis and reconstruction of diurnal flight curves in alienicolae of *Aphis fabae* Scop. *Ann. appl. Biol.* **45**, 682–701.
- Painter, R. H. & Pathak, M. D. (1962). The distinguishing features and significance of the four biotypes of the Corn Leaf Aphid, *Rhopalosiphum maidis* (Fitch). *Proc. XI int. Congr. Ent. (Vienna 1960)*, **2**, 110–5.
- Shaw, M. J. P. (1968a). *Polymorphism in relation to migration by alate alienicolae of Aphis fabae* Scop. Unpublished Ph.D. thesis, London University.
- Shaw, M. J. P. (1968b). Field studies on flight behaviour of *A. fabae*. *Rep. Rothamsted exp. Stn* (1967), 192.
- Taylor, L. R. (1957). Temperature relations of teneral development and behaviour in *Aphis fabae* Scop. *J. exp. Biol.* **34**, 189–208.
- Taylor, L. R. (1963). Analysis of the effect of temperature on insects in flight. *J. Anim. Ecol.* **32**, 99–117.
- Taylor, L. R. (1965). Flight behaviour and aphid migration. *Proc. N. cent. Brch ent. Am. Ass. econ. Ent.* **20**, 9–19.

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