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Long-distance migration of aphids and other small insects in northeast India

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Abstract. Aerial netting at a height of 150 m over West Bengal during November produced evidence for extensive nocturnal migrations of a number of insect taxa, including aphids, leafhoppers, *Nilaparvata lugens* (the brown planthopper) and *Cyrtorhinus lividipennis* (a mirid predator of plant- and leafhoppers). Preliminary trajectory analysis was undertaken for aphids (particularly *Lipaphis erysimi*) overflying the experimental site, and it was estimated from the timing and altitude of flight, and from the winds prevailing at the time, that the long-flying individuals may have originated from sources between 100 and 300 km away to the northeast.

INTRODUCTION

Many economically important diseases of crops which are caused by viruses and mycoplasma-like organisms are spread by insect vectors, particularly aphids, leaf- and planthoppers, thrips and whiteflies (Harris & Maramorosch, 1980). Some of these small insects can undertake windborne migrations over ranges of tens or even hundreds of kilometres. These movements have implications for the epidemiology of disease outbreaks, and have to be taken into account when developing management strategies. However, compared to what has been discovered about vector movement in regions such as Europe, North America and eastern Asia (Johnson, 1969; Thresh, 1983; Kisimoto, 1984; Wiktelius, 1984; Taylor, 1986; Robert, 1987a; Riley et al., 1987, 1991; Irwin & Thresh, 1988; Tatchell & Woiwod, 1990) very little is known of the atmospheric transport of plant disease vectors in the Indian subcontinent, and the phenomenon thus merits investigation.

Windfield trajectory modelling was used by Rosenberg & Magor (1986, 1987) specifically to investigate likely migrations of *Nilaparvata lugens* (Stål), but their results are probably also relevant to the movements of other small migrant insects. Movements in the surface (10 m) and 1.5 km windfields were simulated, and south Asian examples from different seasons were included in the analysis. Rosenberg & Magor (1986) were able to show that in November, under anticyclonic conditions over northeast India and Bangladesh, movements were generally towards the west. However, when eastward-moving depressions were present over northern India, the trajectories indicated movement towards the east or northeast.

We used a complementary approach: a field study covering a short period in a single season, but in which the presence of high altitude migrants was confirmed by aerial trapping. The objective was to determine whether economically important pests and vectors were migrating over West Bengal in November, and if so, to obtain data on the timing and direction of migration, and on the range of movement and possible source areas of the pests. In this paper we focus principally on evidence for long-distance mass migration of aphids, particularly *Lipaphis erysimi* (Kaltenbach), obtained during the study.

METHODS

The field study was carried out in the grounds of the West Bengal Government guest-house at Haringhata, which is adjacent to the Bidhan Chandra Krishi Viswavidyalaya (BCKV) campus at Mohanpur and on the outskirts of the town of Kalyani, about 50 km north-northeast of central Calcutta. Apart from rice, crops sown in the "kharif" (rainy) season included black gram, green gram and cowpea, while early sown "rabi" (post-rainy) season crops included tomato, brinjal, chillies, rape seed, mustard, cabbage and other vegetables.

Between 14 November and 23 November 1992, the insect fauna flying at a height of 130–180 m over the study site was sampled by a net attached to the tethering line of an aerodynamically-shaped balloon (kytoon). The aerial netting equipment and procedures were similar to those described in Riley et al. (1991). Netting was semi-continuous, night and day, except during occasional periods of very light winds at altitude (the net will not sample satisfactorily if the wind speed is below about 3 ms^{-1}). The sampling height was estimated from the length of tethering line paid out and the elevation angle (determined using an inclinometer) subtended by the balloon at the tethering point. Estimates of the wind velocity at the aerial sampling height were obtained from the azimuth of the kytoon tethering line, and the line tension.

At the end of each sampling period, the net was closed by radio-control, the kytoon winched down to ground level, and the detachable bag containing the catch was removed from the net. The bag was then placed in a container with a "Vapona" (DDVP) strip which killed the insects, and these were later sorted and counted. Aerial densities for the various taxa caught in the net were calculated thus:

$$\text{Aerial density} = \text{catch} / \text{volume of air sampled} = \text{catch} / \text{area of net aperture (i.e. } 0.64\ m^2) \times \text{wind run (m)}$$

We attempted to obtain a measure of the abundance and species composition of aphids flying near the ground by using ten yellow pan traps placed at ground level around the aerial trapping site. The traps, each with an area of about 584 cm^2, were emptied at 06.30, 12.00 and 16.30 every day. We also examined the catches of insects in a light trap situated at Mohanpur.

Local meteorological data were available from an observatory at Haringhata farm, near the field site. Synoptic data on winds likely to affect insects flying at or above our trap height were obtained from the India Meteorology Department (IMD), and from the Meteorological Data Dissemination (MDD) service (via Meteosat satellite transmissions). Additional upper air measurements at Calcutta Airport were also made on our behalf by the IMD during the experimental period. Windfield maps were produced for an altitude of 300 m above mean sea level (AMSL) – the standard height nearest to our insect sampling height, and also for the well-documented 850 mbar altitude (about 1,500 m AMSL), for the standard times of 00.00 h, 06.00 h, 12.00 h and 18.00 h GMT. In order to identify likely source areas of the insects caught in the aerial net, back-trajectories were constructed using the streamline-isotach method (Palmer et al., 1955).

Finally, a monostatic non-Doppler sodar sounder was deployed and operated at Haringhata by the Electronics & Communication Sciences Unit of the Indian Statistical Institute, Calcutta, in order to obtain information on atmospheric structure above the experimental site – specifically the height of the night-time temperature inversion.

RESULTS

Species composition of the aerial catches

The different insect taxa caught in the aerial net are shown, as a proportion of the total catch, in Table 1. Apart from minute arthropods (< 0.75 mm in length) which were not identified, the mirid bug *Cyrtorhinus lividipennis* Reuter was the insect most frequently caught, accounting for 20% of the total. Aphididae comprised about 18% of the total catch, the most common species being *Lipaphis erysimi*, the turnip or mustard aphid. Some of the aerial samples also contained the cotton aphid, *Aphis gossypii* Glover, and one sample contained the rice-root aphid, *Rhopalosiphum rufiabdominalis* (Sasaki). Delphacidae (including the brown planthopper, *Nilaparvata lugens*), comprised 6% of the catch, and 3% was composed of Cicadellidae [including the zigzag leafhopper, *Recilia dorsalis* (Motschulsky), and the green leafhoppers *Nephotettix virescens* (Distant) and *N. nigropictus* (Stål)].

Also presented in Table 1 are the taxa taken in the aerial net shown as a proportion of the total caught during the day-time, and during the dusk-to-dawn period. It can be seen that, excluding the unidentified minute arthropods, most taxa were taken largely or exclusively in the dusk-to-dawn samples; spiders, Hymenoptera, and coccinellid beetles are among the few exceptions. Aphids occurred equally commonly in the day and the night samples.

Diurnal variation in insect aerial densities

Table 2 shows the average aerial densities of aphids (mainly *L. erysimi*) flying at about 150 m above the ground, for various periods of the night and day. The values were lowest (2–3 per 10^4 m^3) at dusk and in early evening, significantly ($p < 0.01$, t-test on log mean densities) higher in the later evening, and highest (12–14 per 10^4 m^3) between midnight and dawn. The highest value from an individual sample was recorded between 02.25 and 04.28 h on 21 November when 77 aphids were caught (equivalent to an aerial density of 27 per 10^4 m^3). Day-time aphid densities at the sampling height averaged about 6 per 10^4 m^3.

The diurnal variation in aerial density of the mirid *C. lividipennis* (Table 2) differed from that of the aphids. Densities were very low during the day, but during the dusk period there was a large (× 16) and statistically significant ($p < 0.01$) increase to an average of ca. 11 individuals per 10^4 m^3. Densities of *C. lividipennis* were then maintained at about the dusk level through the night until dawn [the decrease between 21.30 h and midnight (Table 2) was not statistically significant].

The average aerial densities of the leafhopper *Recilia dorsalis* (Motschulsky) flying at different periods of the day and night are shown in Table 3. No *R. dorsalis* were caught at altitude during the day, but there was a peak in aerial density (about 11 individuals per 10^4 m^3) during the dusk sampling period, very probably due to local emigration. Comparison of the dusk period with that between 18.30 h and midnight, showed that there had been a statistically significant ($p < 0.01$) decline in *R. dorsalis* density, and this decline tended to continue after midnight, although the later changes were not statistically significant. The pattern for *N. lugens* (Table 3) was similar, with a significant ($p < 0.05$) increase in density around dusk, followed by a gradual decline until dawn.

TABLE 1. Composition of aerial netting samples taken at Haringhata, Kalyani, 14–23 November 1992.

Order Family	Species	Numbers	All samples	Day samples	Dusk to dawn samples
			%	%	%
Homoptera					
Delphacidae	*Nilaparvata lugens* (Stål)	136	3.17	0.57	3.54
	Other Delphacidae	126	2.94	0.57	3.28
Lophopidae	*Pyrilla perpusilla* (Walker)	2	0.05	0	0.05
Meenoplidae	*Nisia nervosa* (Motschulsky)	14	0.33	0	0.37
Cicadellidae	*Nephotettix virescens* (Distant)	3	0.07	0	0.08
	Nephotettix nigropictus (Stål)	2	0.05	0	0.05
	Recilia dorsalis (Motschulsky)	99	2.31	0	2.64
	Cofana spectra Distant	12	0.28	0	0.32
	Cofana unimaculata (Signoret)	1	0.02	0	0.03
	Empoasca spp.	6	0.14	0	0.16
	Unidentified	21	0.49	0	0.56
Aphididae	*Lipaphis erysimi* (Kaltenbach)	762	17.78	17.14	17.87
	Aphis gossypii Glover	16	0.37	0	0.43
	Rhopalosiphum rufiabdominalis (Sasaki)	13	0.30	0	0.35
Aleyrodidae	*Bemisia tabaci* (Gennadius)	1	0.02	0.19	0
Heteroptera					
Miridae	*Cyrtorhinus lividipennis* Reuter	864	20.23	2.07	22.72
	Unidentified	27	0.63	0	0.72
Nabidae		6	0.14	0	0.16
Pentatomidae		3	0.07	0	0.08
Hydrometridae		2	0.05	0	0.05
Pyrrhocoridae		1	0.02	0	0.03
Unidentified		10	0.23	0	0.27
Thysanoptera					
Thripidae	Unidentified	1	0.02	0.19	0
Ephemeroptera		1	0.02	0	0.03
Orthoptera		22	0.51	0	0.59
Dermaptera		6	0.14	0	0.16
Lepidoptera					
Pyralidae	*Cnaphalocrocis medinalis* Guenée	3	0.70	0	0.08
	Scirpophaga incertulas (Walker)	1	0.02	0	0.03
	Unidentified	2	0.05	0	0.05
Noctuidae	*Anomis* sp.	1	0.02	0	0.03
	Unidentified	1	0.02	0	0.03
Eucosmidae	*Cydea* sp.	1	0.02	0	0.03
Unidentified		9	0.21	0	0.24
Coleoptera					
Carabidae	*Ophionea indica* (Thunberg)	6	0.14	0	0.16
	Unidentified	9	0.21	0	0.24
Staphylinidae		114	2.66	0	3.04
Coccinellidae		7	0.16	0.38	0.13
Chrysomelidae		3	0.07	0	0.08
Hymenoptera		28	0.65	2.26	0.43
Diptera					
Larger Diptera		38	0.89	0	1.01
Culicidae		12	0.28	0	0.32
Spiders		239	5.58	22.03	3.25
Minute arthropods		1,654	38.60	54.61	36.33
Total		4,285			

TABLE 2. Mean aerial densities (number per 10^4 m^3) of aphids and of *Cyrtorhinus livipennis* caught in the aerial net at different periods of the day or night, between 14–23 November 1992.

Sample period		Aphids		*Cyrtorhinus lividipennis*		No. of samples
		Mean	Range	Mean	Range	
Dusk	(c. 16.30–18.30 h)	3.28	0–5.51	11.37	2.21–23.56	8
First part of night	A (c. 18.30–21.30 h)	2.31	0–6.62	11.39	0.83–24.05	6
	B (c. 21.30–00.00 h)	7.38	4.33–14.44	4.65	1.29– 8.62	6
Second part of night	(c. 00.00–04.30 h)	14.54	4.67–23.37	11.38	1.03–16.77	5
Dawn	(c. 04.30–06.30 h)	12.30	5.12–22.98	10.18	4.69–15.22	3
Day	(c. 06.30–16.30 h)	6.33	2.15–17.23	0.69	0– 1.19	5

TABLE 3. Mean aerial densities (number per 10^4 m^3) of *Nilaparvata lugens* and *Recilia dorsalis* caught in the aerial net at different periods of the day or night, between 14–23 November 1992.

Sample period		*Nilaparvata lugens*		*Recilia dorsalis*		No. of samples
		Mean	Range	Mean	Range	
Dusk	(c. 16.30–18.30 h)	2.24	0–5.57	4.53	0–13.79	8
First part of night	(c. 18.30–00.00 h)	1.57	0–4.61	0.75	0– 2.50	13
Second part of night	(c. 00.00–04.30 h)	1.04	0–1.58	0.21	0– 0.39	5
Dawn	(c. 04.30–06.30 h)	0.40	0–1.20	0.14	0– 0.43	3
Day	(c. 06.30–16.30 h)	0.25	0–1.24	0	—	5

Pan trap and light trap data

A larger range of aphid species was caught in the yellow pan traps (Table 4) than in the aerial net, and the species composition was quite different. *L. erysimi*, the aphid most abundant in the net, was less common in the pan catches, and the reverse was true for *A. gossypii*. During the course of each day there was a significant increase in the rate at which aphids were caught in the pan-traps (Table 4). The lowest number were caught during the period up to 06.30 h; the catch for the period up to mid-day was significantly ($p < 0.01$) larger, and that for the afternoon was significantly ($p < 0.01$) larger again.

TABLE 4. Yellow-pan trap catches of aphids from 14 to 23 November 1992 at Haringhata.

	Total catch	Standardized* mean catch at time		
		06.30 h	12.00 h	16.30 h
Aphidinae				
Aphis gossypii	766	2.4	5.8	10.3
Lipaphis erysimi	26	0.3	0.2	0.3
Pentalonia sp.	1	0	0	0.02
Pemphiginae				
Tetraneura spp.	5	0	0.07	0.02
Other Pemphiginae	225	0.2	2.0	2.8
Drepanosiphinae				
Myzocallis sp.	72	0.07	0.7	0.8
Mean for all spp.		3.0	8.7	14.2
Total	1,095			

* Standardized by dividing the catches by number of hours (of daylight) in the trapping period.

No aphids were caught in the light trap during the experimental period. *C. lividipennis* was the most common species caught at the light, a total of 281 individuals being taken. Most were caught during the dusk and early evening (up to 21.30 h), but some were captured later in the night including the midnight to 04.30 h period.

The synoptic situation

During the post-monsoon period in India (October–December) a trough of low pressure is present over the south of the Bay of Bengal (in November this is centred about 7°N), and north of this the prevailing winds are northeasterly trades (Rao, 1981). This wind system determined the displacements of the insects observed by us over West Bengal, which ranged from southwards to westwards. The absence of winds from directions other than from the northeast quadrant meant that we obtained no information on possible relationships between wind direction and the numbers of insects in flight.

Winds during the observational period

The surface winds during the observational period were often very light or calm, but at the aerial netting height of about 150 m the mean wind speed (calculated from pilot balloon data from Calcutta airport) was 4.20 ms^{-1} ± 1.75 (s.d.) usually from the northeast or north-northeast (mean direction = $14^{\circ} \pm 42^{\circ}$). Late morning wind speeds at 150 m tended to be weaker (2.9 ms^{-1}) than those of late evening and dawn (4.8 ms^{-1}). Variations in speed at the sampling height were, of course, influenced by synoptic events. For example, the presence of a cyclonic storm in the north of the Bay of Bengal strengthened the winds at the sampling height between 19–21 November.

Judging from the pilot balloon data from Calcutta, wind velocities at 300 m above ground were very similar to those at our sampling height of 150 m. This similarity allowed us to use 300 m wind data, available from other synoptic stations, in the construction of back-trajectories for the sampled insects.

At the 850 mbar level (approximately 1.5 km), winds were usually from the northwest with a mean speed of 4.7 ms^{-1} ± 2.0 (s.d.). There was a spell of lighter and more variable winds at this level on 19 and 20 November when the upper westerlies were disrupted by the aforementioned cyclonic disturbance. On the evening of the 20 November, for example, winds blew from the east.

Altitude of the surface temperature inversion

It is advantageous to take aerial netting samples at an altitude corresponding to the top of the surface temperature inversion (if one forms), because there is often a local maximum in the wind speed there (in contrast to lighter winds or calm conditions within the inversion) and also because insect concentrations sometimes occur at this height (Drake & Farrow, 1988). The returns from the sodar equipment deployed at our site regularly showed the development of a discontinuity at approximately 120–130 m during the early evening, and this was attributed to the top of the surface temperature inversion. The discontinuity tended to rise as the night progressed, and typically reached 180–190 m by dawn. It rose to about 350 m over the next few hours, before breaking up into convective plumes.

DISCUSSION

During the daytime, airborne insects can be carried up to altitudes of hundreds of metres by convective motion of the atmosphere (Johnson, 1969). At night, during undisturbed weather, there is no convective lift, and if nocturnal flyers are to maintain their altitude they must do so by continuous active flight. For example, inert *Aphis fabae* Scopoli sink at about 0.8 ms^{-1} even with their wings extended (Thomas et al., 1977), and so in the absence of wing flapping they would descend to earth from 1,000 m altitude in only 20 minutes. The capture of insects at altitude during the course of the night thus demonstrates that they were engaged in deliberate, persistent locomotory behaviour, i.e. that they were migrating.

Because the wind speed at altitude will generally be faster than the flying speed of small insects, they will tend to be displaced downwind, irrespective of their orientation, and in this sense can be described as windborne. Estimates of their migratory flight paths can thus be obtained if the winds at their flight altitudes are known, and if one also has information about the timing of their take off and about their flight duration.

Pan trap catches and the timing of aphid take-off

Extensive evidence in the literature convincingly suggests that migratory aphids take off during daylight (e.g. Lewis & Taylor, 1964; Johnson, 1969; Dry & Taylor, 1970; Robert, 1987b), and that emigration after dusk is inhibited by below-threshold illumination levels. Dixon & Mercer's (1983) finding that a proportion of second generation *Drepanosiphum platanoides* (Schr.) took off after dark does not contradict this conclusion, because the observed nocturnal take-off was interpreted as an adaptation for "trivial" flight during calm evenings.

Yellow pan traps are thought to be adequate to assess aerial populations of aphids near the ground (Robert et al., 1988). Although the traps are unlikely to catch individuals taking-off on long-range migratory flights (Hardie, 1989), they probably attract aphids engaging in local "trivial" flights, as well as any descending after longer-distance migration. The rate at which our pan traps caught aphids increased throughout the day (Table 4), and we interpret this to mean that there was a cumulative build-up in aphid flight activity at low altitude. The build-up was presumably caused by continuous recruitment and take-off of flight-mature aphid alates (Johnson, 1969). This apparent pattern of take-off during the day was common to all the aphid species caught in the traps, and we take it to imply that any aphid emigratory flights probably also began during the daytime. While this interpretation is not conclusive in itself, it *is* consistent with the general view that aphids begin their migratory flights during the daytime.

We also note that the absence of aphids in the light trap catch at Mohanpur may indicate that there was little aphid flight activity at low altitude during the night.

Aphid flight duration

The evidence discussed above suggests that the aphids caught in our aerial net between midnight and dawn had probably started their flights at sometime during the previous day. On this assumption, their flights would have been of at least 7 hours duration (sunset was about 16.50 h and first light was about 5.20 h), and some may have been as long as 20 hours if migrants had taken-off in mid-morning. Continuation of flight into the night by aphids and other small insects is known to occur elsewhere (Berry & Taylor, 1968;

Farrow, 1982; Taylor, 1986), and it may be common on warm nights in continental areas. Nocturnal flight will clearly expand the aphids' migratory ambit significantly, especially if the insects encounter the fast low-level wind jets which frequently develop at night above a temperature inversion (Berry & Taylor, 1968; Drake & Farrow, 1988).

It may be that nocturnal migrations are artificially prolonged when there is a strong surface temperature inversion, because flying aphids could be inhibited from descending into the layer of comparatively cold air near the ground (Farrow, 1986). This does not seem likely in the present study, as on the nights when large numbers of aphids were flying, the difference between the temperature at the aerial sampling height and the surface was only about 1°C.

The intensity of aphid migration

The increase in our aerial net catches later in the night appears at first sight to imply that the more prolific sources of flight-ready aphids were more distant from our trapping site. However, the increase might equally reflect changes occurring in aphid altitudinal distribution during the course of the night, such as to progressively concentrate migrants near the sampling height. In any event, the aerial densities of nocturnally migrating aphids found by us at Kalyani and in another study at Hyderabad in central India (Reynolds & Wilson, 1989), were much higher than those found at altitude in Kansas in the USA, and in Bedfordshire in the UK (Table 5). The data in Table 5 were not all obtained at the same altitude, so it would be unwise to attribute too much significance to the differences between trapping sites, but it does seem clear that nocturnal aphid migration in India is at least as significant as that found elsewhere, and it may play a role in the ecology of several species.

TABLE 5. Comparison of the aerial density of aphids flying at altitude at night.

Time of night	Height (m)	Density (nos. / 10^4 m^3)			Reference (and location)
		Mean	Min.	Max.	
00.00–04.30	c. 150	14.5	4.7	23.4	Present study (West Bengal, India)
01.00–04.00	610	0.29	0	0.54	Berry & Taylor, 1968 (eastern Kansas, USA)
various between 18.00–06.15	c. 100	1.7	0	8.8	Reynolds & Wilson, 1989 (near Hyderabad, India)
01.00–04.00	305	0.19	0	0.94	Berry & Taylor, 1968 (Bedfordshire, England)

Back-tracking of aphid migrants to possible source areas

Back-trajectories were constructed for the occasions when large numbers of aphids were caught after midnight in the aerial net. As mentioned above, we concluded that the aphids had probably taken off at sometime during daylight the previous day, and this suggested that a flight duration of 15 hours was plausible. We used windfield maps for an altitude of 300 m, the altitude nearest to our trapping height of 150 m for which wind data were available. This procedure was unlikely to introduce significant errors because there was generally very little difference in wind velocity between 150 and 300 m (see above). Judging from radio-soundings at Calcutta, air temperature during the observational period was usually above 16°C even at 1,500 m, so we had no reason to assume that aphids might not also be flying much higher than our net (c.f. Glick, 1939; Berry & Taylor, 1968).

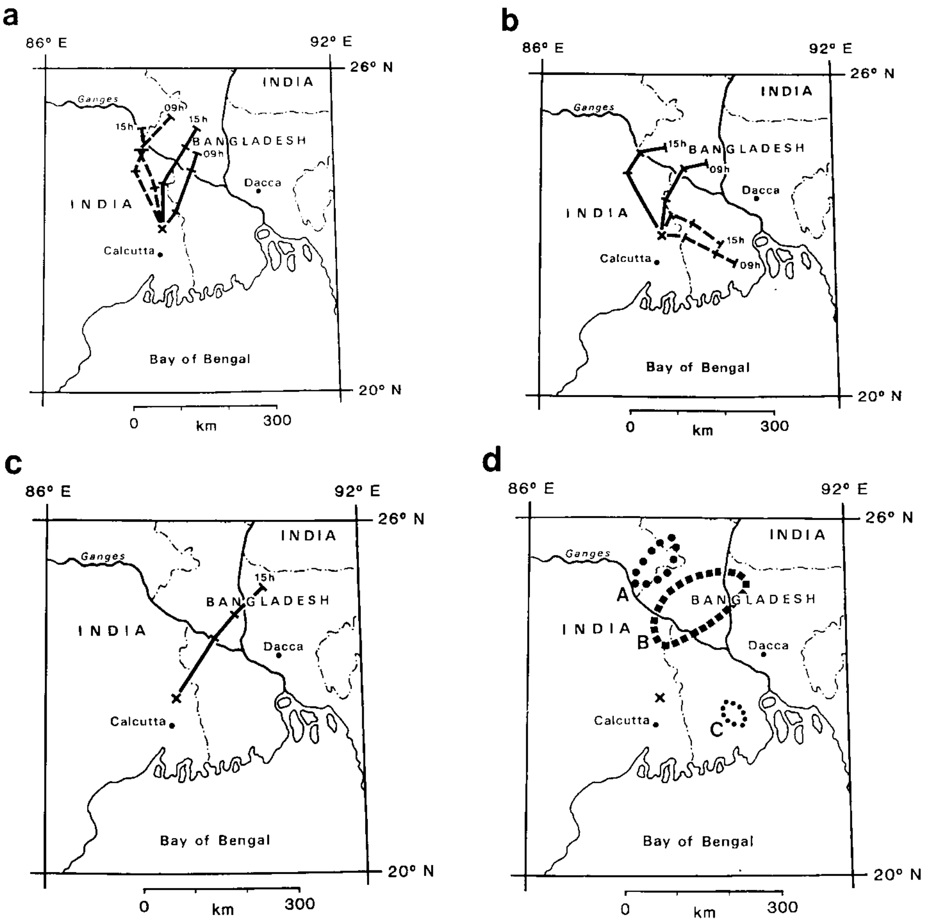

Fig. 1a–c. Specimen back-trajectories showing estimated flight-paths for aphids migrating over the aerial netting site at Haringhata, near Kalyani. a: on the night of 16–17 November; b: 20–21 November; c: 19–20 November 1992, at flight altitudes of 300 m (solid lines), and ca. 1,500 m (broken lines). Trajectories are marked with the time of take off, and each "leg" indicates 5 hours of flight. Thus insects presumed to have taken off at 09.00 h, arrived over the netting site at midnight, and those which took off at 15 h, arrived at 06.00 h. (The trajectory for the 1,500 m level on 19–20 November is not included as winds were light at this height).

Fig. 1d. Putative source areas for aphids arriving at the aerial netting site at Haringhata, either at midnight or at 06.00 h on the nights of 15–16, 16–17, 19–20 and 20–21 November, assuming 15 hour migrations. The areas marked encompass the take-off points for (A) the 1,500 m trajectories for 15–16 and 16–17 November, (B) the 300 m trajectories for all four nights, and (C) the 1,500 m trajectories for 20–21 November. The position of the netting site is indicated by the cross.

Therefore, as an additional, more speculative exercise, we also computed back-trajectories using the readily-available data for the 850 mbar (approximately 1,500 m) level.

Figs 1a–c show specimen trajectories for those insects which had arrived over the netting site at midnight and at 06.00 h local time. These trajectories probably represent the *maximum* distances travelled nightly by aphids in this area of India, and we do not imply that the bulk of the population necessarily moved so far. The 300 m altitude trajectories indicated that migrants came from an area north-northeast of the trapping site, bounded approximately by Baharampur in West Bengal, and Pabna, Naogaon and Jamalpur in Bangladesh (Fig. 1d).

Synoptic wind data for the 850 mbar level indicates that any aphids flying at this height on 15–16 and 16–17 November, would have come from a source area to the north of the netting site between English Bazar and Dinajpur (Fig. 1d). On the other hand, any flying for 15 hours at the 850 mbar level on 20–21 November would have come from the Khulna area of Bangladesh, to the east.

The ecological relevance of the aphid movements

In India, *L. erysimi* is virtually absent from the plains during the hot summer (Kranz et al., 1977), although small numbers may sometimes persist in especially favourable places (Sidhu & Singh, 1964), and the species is believed to reinvade lowland cropping areas each autumn from the hills (Narayanan, 1958; Kranz et al., 1977). The long-distance migration into the Calcutta area from the northeast, deduced in the present study, is clearly consistent with this hypothesis. There are also putative movements of aphids on the southwesterly winds in spring, and these would tend to carry the insects from the plains back towards the hills (Narayanan, 1958; S. Mukhopadhyay, unpublished). Gurung et al. (1993), working in the Darjeeling hills, certainly found evidence of a redistribution of alates in other aphid species early in the year. The ecological significance of these seasonal migrations is not clear, but they may well be adaptive if they allow aphids like *L. erysimi,* which breed parthenogenetically in the tropics, to avoid the high summer temperatures of the plains and the low winter temperatures of the upland areas. A simple model of *L. erysimi* "forward" and "return" migrations between hills and plains would probably be over-schematic. Even allowing for the seasonal reversal of prevailing winds, aphids are undoubtedly carried in a wide variety of directions and so only a proportion of the migratory population would reach habitats which are, for various reasons (including altitude), seasonally favourable. The high reproductive rates of the successful immigrants would help to compensate for the mortality incurred during migration.

The presence in our post-midnight aerial samples of *Rhopalosiphum rufiabdominalis* and *Aphis gossypii* indicated that, like *L. erysimi,* these species were undertaking long-range movements. This is perhaps not surprising because *R. rufiabdominalis* is known to engage in nocturnal windborne migration over the Hyderabad area of central India (Reynolds & Wilson, 1989), and captures at sea have shown that both species have at least the potential for long flights: more than 24 hours for *R. rufiabdominalis*, and 18 hours for *A. gossypii* (Rutter & Mills, in prep). Moreover, movements of *A. gossypii* out of upland areas in northeast India in November seem very plausible because dispersive alates of this species (and others) have been collected in pan traps (at heights of 9–12 m) in the Darjeeling hills at this time (Gurung et al., 1993).

Short- and long-range movement in flying aphids has been recently reviewed by Loxdale et al. (1993). Although several examples of long-distance migration are presented, the authors tentatively conclude that these movements are infrequent or exceptional, may have been atypically prolonged by flight over unsuitable habitats (e.g. water or desert), and are of little biological importance compared to short-range movements. In the present study we found substantial densities of aphids (particularly *Lipaphis erysimi*) in flight after dark and engaged in long-distance migration. These prolonged migrations did not seem to be unusual, in that they were detected on most of the observational nights, they were not over hostile terrain, and large numbers of individuals were involved. We conclude from this that in West Bengal at least, long-range aphid migration is not atypical. We do, however, concur with the view of Loxdale et al. (1993) that the ecological significance and economic importance of long-range movements by aphids require clarification.

Migratory flight in other species

Cyrtorhinus lividipennis

The mirid bug, *C. lividipennis* is an important predator of plant- and leafhopper pests of rice in the tropics (for India, see e.g. Pophaly et al., 1978). It is often found migrating at the same time and altitude as its prey, and in several aerial netting studies in the tropics it was one of the species most commonly caught (Riley et al., 1987; Reynolds & Wilson, 1989, and the present study).

The changes which we generally observed in insect aerial densities through the night, at our sampling altitude, were probably the cumulative result of several factors. For example, there were probably differences in the emigration rates of source populations sequentially further upwind; there would certainly be differences in the flight endurance of individual migrants, and changes may have occurred in the distribution of flight altitudes as the night progressed. The relative invariance of *C. lividipennis* aerial density during the night, which we observed, seems to have arisen because these factors happened to produce compensatory effects.

In the present study we found that very few individuals of *C. lividipennis* were aloft during the day, but the species became active at light in early evening. These observations suggest that *C. lividipennis* in West Bengal probably begins migratory flight at dusk – a result similar to that found for the species in the Philippines (Riley et al., 1987). If this is the case, our aerial netting data shows that flight durations of more than 6 hours were common. For example, the individuals caught after 02.25 h on 21 November would presumably have flown for 9.5 hours at least. It is just conceivable that those caught in the 04.30–06.30 h samples might have taken off at dawn, and been in flight for only a few minutes, but we know of no evidence to suggest that *C. lividipennis* emigrates at dawn.

In contrast to the long-flying behaviour we report here, the aerial density of *C. lividipennis* in the dry season in the Philippines has been found to decline very sharply after dusk, and very few individuals were caught aloft at dawn (Riley et al., 1987). Thus there, and possibly also in Malaysia (Lim, 1978; Ooi, 1979), the species seems to confine its migration largely to short flights around dusk. There is some evidence that long migrations of *C. lividipennis* occur over central India as well as over West Bengal, because substantial numbers (up to 28 per 10^4 m^3) have been detected at altitude late in the evening on some occasions (Reynolds & Wilson, 1989).

Leafhoppers

The leafhoppers *Recilia dorsalis* and *Nephotettix virescens* found in our aerial samples are known to have a well-defined peak of take-off around or just after sunset (Perfect & Cook, 1982). Thus the large fall in density of *R. dorsalis* after the dusk netting period showed that most individuals of this species probably flew for only 1.5 hours or less (i.e.

between 17.00 and 18.30 h). However, a few were caught after midnight, and these had presumably flown for about 7 hours. The five specimens of *N. virescens* and *N. nigropictus* in our aerial samples were all caught during either the dusk, or the post-dusk period, so it seems likely that the majority of these insects, like *R. dorsalis*, flew for less than 1.5 hours.

At least some individual *N. virescens* are capable of prolonged flight, as they have occasionally been caught far out at sea (see references in Riley et al., 1987), but the species is often considered rather sedentary (Kiritani, 1974). Aerial trapping over land probably gives a reasonable indication of more typical migratory duration, and Riley et al. (1987) found that in the Philippines, the vast majority of individuals were caught in an aerial net during a relatively short period (ca. 1 hour) around the time of the dusk take-off. The similar, but more limited data available from the present study, suggests that in India, both *N. virescens* and *N. nigropictus* flew at altitude for relatively short periods only. This conclusion may be compared with the results of Bowden et al. (1988) who analysed catches of *N. virescens* and *N. nigropictus* from light traps at Kalyani (near the site of the present study) and found that 85% of flight activity occurred in the first 5 hours after sunset.

Nilaparvata lugens

Tropical *N. lugens* also has a peak of emigration around or just after sunset (Perfect & Cook, 1982; Perfect et al., 1985; Padgham et al., 1987; Riley et al., 1987), and the take-off of migrants very probably produced the increased aerial densities of this species which we observed around dusk. After the dusk sampling period, the density of *N. lugens* declined slowly through the night, suggesting that there was a much greater proportion of long-flying individuals in this species than in, for example, *R. dorsalis*. The catch of *N. lugens* after 02.25 h on 21 November (when the post-midnight sample was divided into two parts) indicates that some individuals were flying for at least 9.5 hours.

N. lugens is well known to be a long-range windborne migrant in East Asia, and the species moves northward from the tropics (Cheng et al., 1979; Kisimoto, 1987) to reinvade temperate regions of China, and then Korea and Japan, every year. Southwards "return" movements occur in autumn, and in eastern China these have been studied in detail by radar. The radar studies showed that planthopper movements could be intense, with vast numbers of planthoppers emigrating in the late afternoon-to-dusk period and continuing in migratory flight for several hours after dark (Riley et al., 1991, 1994). Peaks of emigration were also detected at dawn, but the subsequent mass migrations were of much shorter duration than those following the dusk peak. Radar studies in the Philippines have demonstrated, by contrast, that although there were well-defined peaks of take-off by rice insects (including *N. lugens*) for about 30 minutes at dusk and dawn, flight at altitude was minimal at other times and so migratory distances were probably short (Riley et al., 1987). Ground-trapping studies in the Philippines also suggested that *N. lugens* moved short distances (Perfect & Cook, 1987; Loevinsohn, 1991). Predominantly short movements are to be expected in the humid tropics, because rice (cultivated, ratoon or wild) is present all year round and movements over a few kilometres would be enough to ensure maintenance of the *N. lugens* population. In addition, long-fliers may be particularly uncommon on tropical islands far from continents because emigrants leaving the islands are unlikely to be replaced to any significant degree by long-flying immigrants from remote overseas sources.

Comparison of the results from the Philippines and China suggests that short-range migration tends to predominate in the tropics, while longer-range movement is the norm in temperate regions. However, this is not the whole story, because the results of the present study, and those reported by Reynolds & Wilson (1989), suggest that long-distance movements by *N. lugens* occur in tropical areas in India. We also note that the extreme south of China and adjoining areas of Indo-china, which are tropical, must harbour a proportion of long-flying individuals in order to initiate the colonisation of temperate China every year. Overall, we conclude that long-distance migration of *N. lugens* is most adaptive in temperate continental areas, moderately adaptive in tropical continental areas (especially those with a more pronounced dry season) and least adaptive in archipelagos (e.g. Philippines) or peninsulas (e.g. Malaysia) in the humid tropics.

CONCLUSIONS

This short study provided convincing evidence for medium- and long-range migration by a number of important aphid, leaf- and planthopper vectors of plant viruses. These observations represent the first direct demonstration that mass movement of vectors occurs at altitude over northeast India. We do not, however, wish to over-emphasise the importance of the long-flying migrants: as Taylor (1986) points out for aphids, migration distances probably form a continuum in which the middle distance may be the most important. In the present study, we have no idea of the proportion of migrants which may have travelled medium or short distances and landed before they reached our netting site.

More generally, this study shows how intensive, limited duration observations of insect movement at altitude, can be used to improve our understanding of the atmospheric transport of important pests and of disease vectors of agricultural crops in the tropics. Information of this sort should make it possible to establish whether seasonal vector migration patterns have a significant role in the epidemiology of plant disease outbreaks in this region.

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