

## Variation in behavioural migration in aphids

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**Abstract.** The behaviour of *Aphis fabae* during maiden flight in an automated flight chamber was assessed by their response to the intermittent presentation of a plant-like visual target. As shown previously, alate virginoparae were much more responsive to the target, i.e. indicating foraging flight, during the initial part of maiden flight than were gynoparae. Virginoparae initiated foraging flight after a short behavioural migratory period, i.e. the initial period of flight when the aphid remains unresponsive to the target, (on average  $8 \pm 5$  min) while gynoparae undertook a longer migratory flight (on average  $102 \pm 19$  min). However, if starved for 24 h, under conditions that did not allow flight, both aphid forms initiated foraging flights more readily and the period of behavioural migration was reduced ( $0.7 \pm 0.3$  vs  $36 \pm 11$  min, virginoparae vs gynoparae). This observation indicates that the initiation of foraging flight, and thus the duration of migratory flight, can be influenced by factors other than flight per se.

### INTRODUCTION

Long distance movement can be achieved by flying aphids ignoring cues associated with resource items that would initiate landing (e.g. host plant or a mate; i.e. behavioural migration) or by aphids actively seeking a resource item (i.e. foraging) but where the resource is not apparent or is unattainable as climatic conditions are unsuitable for directed flight/landing. From an ecological view, migration is the long distance movement of individuals or populations and the means by which this movement is effected is not important. However, from the behavioural view it is crucial to try and distinguish how such movement is effected by the individual insect (Kennedy, 1985). Behavioural migration in aphids is a period of persistent, skyward flight during which visual cues from host plants are ignored (David & Hardie, 1988; Nottingham & Hardie, 1989). It occurs during the initial part of maiden flight and is followed by a period when plants prove visually more attractive than sky. This latter period can be considered as the foraging, or plant-responsive, flight phase and will eventually terminate on settling. An automated flight chamber, with intermittent presentation of a visual, plant-mimicking cue, allows investigation of behavioural migration and the measurement of its duration. It has been shown that, in two host-alternating aphids, the summer alate virginoparae exhibit a short or non-existent behavioural migration, while autumn gynoparae have a long migratory period (David & Hardie, 1988; Nottingham & Hardie, 1989; Nottingham et al., 1991). This paper will address these differences and explore the initiation of foraging flight and the reciprocal change in duration of behavioural migration.

### MATERIALS AND METHODS

A clone of *Aphis fabae* Scopoli was reared on tick beans, *Vicia faba* L., at 15°C. Alate virginoparae were obtained from cultures where young larvae had been crowded on bean stipules (growing tips

removed) under long-day conditions (LD 16 : 8) while gynoparae were obtained by transferring insects to short days (LD 12 : 12) (Hardie, 1980).

The response of free-flying aphids to an intermittent plant-mimicking green target was observed in an automated flight chamber (David & Hardie, 1988). This comprised a bright overhead light source, which induced the aphids to fly upwards, and a downward flowing air current which countered the insects upward movement. A video-computer link automated the regulation of the air flow and held the insect flying at the level of a side-wall-mounted, circular, translucent target screen which was illuminated by a plant-green light for 2.5 s during each minute of flight. The track of the aphid was automatically logged by the computer and used for the analysis of the flight behaviour.

Aphids were collected immediately after first take-off and either transferred to the flight chamber, where they effectively undertook their maiden flight, or were starved in dark conditions over damp sand for 24 h. Holding in the dark ensured that the insects did not attempt flight before their delayed maiden flight in the chamber.

Behavioural migration was measured as the initial period of flight during which the green target was ignored and the aphid continued to fly to the overhead light. Attraction to the illuminated target was judged by analysis of the horizontal component of the flight track in two ways :

A) THE TIME OF CLOSEST APPROACH TO THE TARGET. If this coincided with the time of target illumination then the insect could be judged to have shown a preference for the green target over the overhead light. A closest approach during the five second period covering the 2.5 s of target illumination and the succeeding 2.5 s was considered coincident with target presentation (Hardie et al., 1989).

B) THE DISTANCE MOVED TOWARDS THE TARGET DURING ILLUMINATION. This was judged by comparing the closest approach to the target in the 5 s period immediately prior to illumination with the 5 s covering illumination (David & Hardie, 1988).

Previous studies considered persistent target approaches to occur when the time of closest approach coincided with target illumination in 4 of 5 consecutive minutes of flight (Nottingham & Hardie, 1989; Nottingham et al., 1991). At this point in time behavioural migration was considered terminated. In the present study 3 coincidences out of 4 minutes were assessed as the end of behavioural migration as a slightly less rigorous

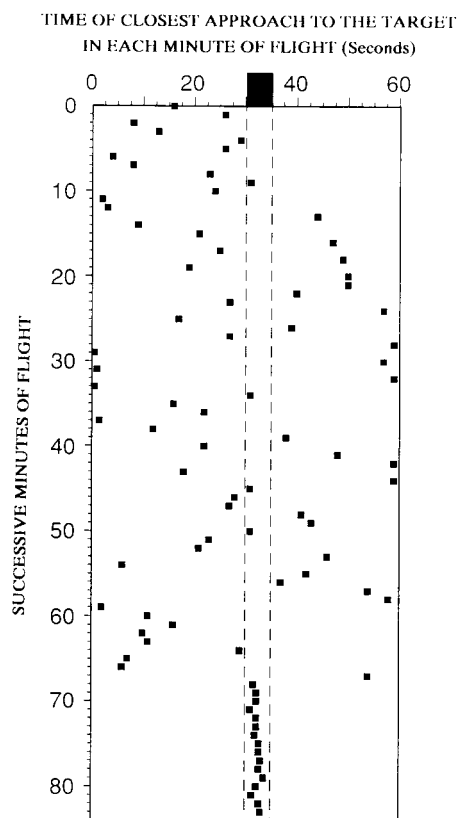


Fig 1. Eighty four minutes of the maiden flight of an individual gynopara, starved in darkness for 24 h, showing the times of closest approach (solid squares) to the target for each flight minute. Target illumination was from 30–32.5 seconds into each minute of flight, movement towards the target was indicated by coincidence of the time of closest approach and the 5 s period including target illumination plus the following 2.5 s (dashed lines). The initial period of flight shows a random distribution of closest approaches indicating that the target is ignored but behaviour switches at minute 68 and the target proves consistently more attractive than the overhead light.

measure of persistent target approach. In addition, the mean movement towards the target was calculated over the first 30 min of flight. The latter approach gives an overall impression of target attractiveness during this initial flight period. In some insects it includes migratory and foraging behaviour.

## RESULTS

An example of the closest approach analysis is shown in Fig. 1. This individual gynopara had been held for 24 h prior to flight, persistent movement towards the green target began after 68 min of flight when the moment of closest approach to the target consistently coincides with target presentation. The durations of behavioural migration, as judged by 3 coincidences out of 4 flight minutes, are shown for alate virginoparae and gynoparae in Table 1. There is a decrease in the period of migration in insects held for 24 h but this is only significant for gynoparae.

TABLE 1. Arithmetic means (SEM) and ranges of behavioural migration measured in alate virginoparae and gynoparae immediately after first take-off and after holding for 24 h before flight.

Period held (hours)	0		24	
Migratory period (min)	Mean	Range	Mean	Range
Virginoparae	$8 \pm 5$	0–77	$0.7 \pm 0.3$	0–3
Gynoparae	$102 \pm 19$	0–332	$36 \pm 11$	0–114

Mann-Whitney U test indicated a significant difference between gynoparae flown immediately and after 24 h ( $P < 0.01$ ) but not between virginoparae,  $n = 15$  except for gynoparae flying immediately where  $n = 25$ .

Differences in flight behaviour can also be seen when the numbers of times that the moment of closest approach to the target coincides with target presentation are compared over the first 30 min period of flight (Fig. 2). There are significant differences between

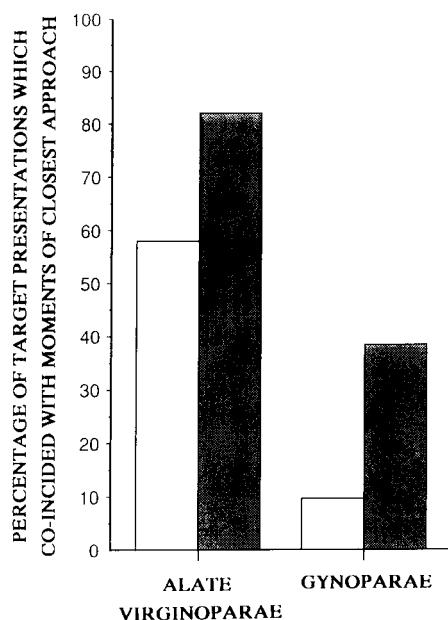


Fig. 2. The coincidence of closest approach to the target and the time of illumination, over the first thirty minutes of flight, for virginoparae and gynoparae flown both immediately after the teneral period (open) and after being held for 24 h (stippled). Target presentations numbered 750 for immediately flown gynoparae (25 aphids) and 450 in other cases (15 aphids). Chi-squared tests demonstrate significant differences between immediately flown and 24-h held insects ( $P < 0.001$  for virginoparae and gynoparae).

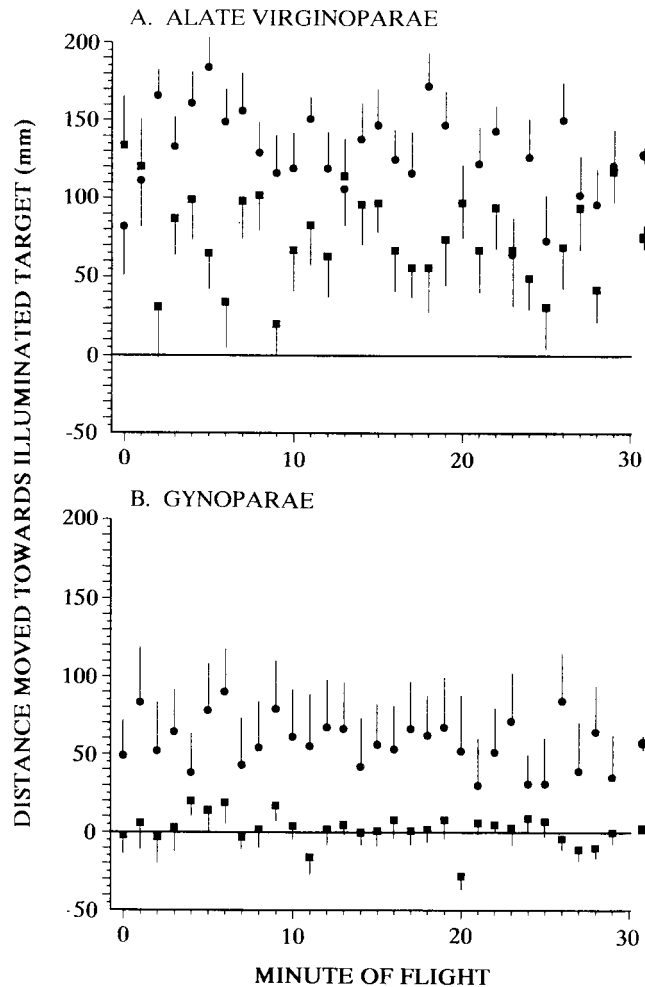


Fig. 3. The mean (SEM) approach to the illuminated target by virginoparae (A) and gynoparae (B) during the first thirty minutes of flight. Squares indicate insects flown immediately after the teneral period, circles indicate insects flown after being held for 24 h. The mean (SEM) of the mean distance moved towards the target for each minute of flight is shown to the right. The differences between immediately flown and 24-h held insects are significant (Student's t-test,  $P < 0.001$  for virginoparae and gynoparae).

aphids flown immediately and those held for 24 h. Similarly, if the movement towards the illuminated target is considered there are significantly larger displacements towards the target in the older aphids (Fig. 3). These differences hold for both virginoparae and gynoparae.

#### DISCUSSION

Previous studies in the automated flight chamber have shown that during maiden flight, immediately after the teneral period, *Aphis fabae* gynoparae undertake a prolonged

behavioural migration while alate virginoparae show either a shorter migration or none at all (David & Hardie, 1988; Nottingham & Hardie, 1989).

During the foraging flight phase both gynoparae and virginoparae respond identically to targets illuminated with spectral light of different wavelengths even though they utilise different host plants (Hardie, 1989). The reason(s) for the difference in flight behaviour between gynoparae and virginoparae is not immediately apparent. There seems to be no advantage for host-plant location although this behavioural difference may relate to the tendency of gynoparae to fly at higher altitudes than virginoparae and Tatchell et al. (1988) have suggested that this may assist landing on the primary host trees which are taller than the herbaceous, secondary hosts. In addition, the increased readiness of gynoparae to take-off and to fly for long periods prior to landing will ensure sexual females are not produced on the inappropriate natal host and will enhance genetic mixing during this sexual phase of the life cycle.

The earlier appearance of foraging flight in aphids starved for 24 h, without the opportunity to fly, indicates that the period of behavioural migration can be influenced by factors other than flight. In the field, climatic conditions, such as low temperature or high winds, that prevent flight might also reduce the duration of behavioural migration although the influence of feeding vs starvation during delayed flight has yet to be assessed. The mechanism involved in initiating foraging flight is not known although it seems possible that a decrease in energy reserves (carbohydrates or lipids) after a period of flight or starvation might provide the stimulus. However, this idea is countered by the fact that foraging flight is initiated earlier in gynoparae treated with juvenile hormone or anaesthetised under nitrogen or carbon dioxide (Hardie et al., 1989). It seems unlikely that these treatments will affect the metabolism of energy reserves.

There is a large variation in duration of migratory behaviour between clonal individuals, even when rearing conditions are as close to identical as it is possible to make them in the laboratory. The variation appears to be another expression of polyphenism which could be advantageous, spreading the risk of migration to clone survival between sisters attempting longer- and shorter-distance movement.

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