Variability and genetic basis for migratory behaviour in a spring population of the aphid, *Aphis gossypii* Glover in the Yangtze River Valley of China

X.D. Liu[1]*, B.P. Zhai[1], X.X. Zhang[1] and H.N. Gu[2]

[1]Department of Entomology, Nanjing Agricultural University,
Nanjing 210095, China: [2]CSIRO Entomology, Black Mountain Laboratories,
Clunies Ross Road, Canberra, ACT 2601, Australia

Abstract

The population dynamics, development of gonads, takeoff and flight behaviour of *Aphis gossypii* Glover were investigated in order to test whether there was variation of migratory ability in the spring population. Field surveys showed that not all the aphids overwintering on hibiscus migrated to the secondary host plants, and the host-alternating and host-specific life-cycle forms coexisted in Nanjing, China. Substantial variation in flight capacity of winged individuals, development of gonads and takeoff behaviour were found within the spring population. The frequency distribution of flight duration and the number of ovarioles per individual alatae exhibited two peaks, representing the migratory and sedentary genotypes, respectively. Significant response to directional selection on takeoff behaviour demonstrated the additive genetic component of this variation. Selection for 'takeoff' individuals caused a significant increase in takeoff angle from 39.8° in the first selection to 68.7° in the fifth; and, hence, screened out the migratory genotype (M), while selection for the sedentary individuals increased the rate of non-takeoffs significantly, and screened out the sedentary genotype (S). The reciprocal cross, M♀ × S♂, produced hybrid offspring performing significantly steeper takeoff angles compared with those from the cross S♀ × M♂, suggesting the presence of a maternal effect. On the other hand, takeoff rate was ranked as M♀ × S♂ = S♀ × M♂ > M > S, involving no sex-linkage and maternal effect. The coexistence of host-alternating and host-specific life-cycle forms of *A. gossypii* on the primary host has, as deduced from the present studies, a genetic basis.

Introduction

There are two types of life cycle in aphids: autoecious (host-specific) and heteroecious (host-alternating). Autoecious species live on one or a few species of a particular plant

genus, whereas heteroecious species usually spend the summer on herbaceous plants and pass other seasons on a woody host (Dixon, 1998). The cotton-melon aphid, *Aphis gossypii* Glover, has a heteroecious life cycle in the Yangtze River Valley of China. Populations overwinter mainly on the hibiscus plant, *Hibiscus syriacus* L., and in late spring and early summer migrate from the primary (winter) hosts to secondary (summer) hosts, including various vegetable, horticultural and field crops, such as cucurbits, chrysanthemum and cotton. After more than 20 parthenogenetic

*Author for correspondence
Fax: +8625 84395242
E-mail: liuxd@njau.edu.cn

generations on the secondary hosts, *A. gossypii* populations produce winged sexuparae in autumn, which then undergo the reverse migration to the primary host where the sexual forms mate and cold hardy overwintering eggs are laid (Ding & Su, 2002). Thus, seasonal migration plays an important role in the heteroecious life cycle and population process.

Empirical studies have shown that cotton-melon aphids possess a great potential for migration between the primary and secondary hosts, and some individuals can even ascend beyond the boundary air layer and be transported by air current or wind over large geographical distances (Isard *et al.*, 1990; Reynolds *et al.*, 1999). Tethered flight tests have further demonstrated that winged *A. gossypii*, collected from the primary host *H. syriacus* in Nanjing, China, can fly continuously for some 4–6 km under laboratory conditions and most such aphids had gonads with less than seven ovarioles each (Liu *et al.*, 2003b). However, it is unclear whether there is differentiation in flight capacity within *A. gossypii* spring populations, with migratory genotypes leaving the primary host whilst non-migratory ones remain on it. In order to address these issues, the present study was conducted to: (i) investigate the possibility of differentiation in gonad development and flight tendency in a spring population; and (ii) examine the genetic basis for the intra-population differentiation of *A. gossypii*.

Because of their small body size, aphids can generate only relatively small flight forces (Byrne *et al.*, 1988), and their displacement relative to the ground during flight is largely governed by air movement (Taylor *et al.*, 1979). Therefore, the takeoff behaviour leading to ascent beyond the boundary air layer where such small insects are carried by wind over large distances is often tested to measure the potential for migration in aphids (Gatehouse, 1997; Dixon, 1998). However, the takeoff behaviour of aphids is highly variable among individuals. Such variability is often related to the number of ovarioles in their gonads. For instance, aphids with few ovarioles are known to take off more readily and at a steeper angle than those with more ovarioles (Walters & Dixon, 1983; Zhang & Wang, 1991; Dixon, 1998; Liu *et al.*, 2003a). In our study, we, therefore, conducted field observation on a spring population, measured the tethered flight capacity, takeoff frequency and takeoff angle of winged *A. gossypii*, sampled from the spring population on hibiscus trees, and examined the number of ovarioles in their gonads to assess population differentiation related to migratory potential. The genetic basis of population differentiation in migration was also investigated through bi-directional selection and cross-breeding experiments.

Materials and methods

Field survey on a spring population

Field surveys of *A. gossypii* populations were conducted on 15 hibiscus trees on the campus of Nanjing Agricultural University, China (32°04′N, 118°50′E). Five 20-cm-long branches with *A. gossypii* were selected from each of these trees and labelled in the first observation. Aphids on these labelled branches were surveyed every four to seven days from June to October in the years 2003, 2004 and 2006. The number of *A. gossypii* populations found during the whole of August was very important because, if the aphids on hibiscus can live through this month, they probably have the ability to undergo the host-specific life cycle on the primary host plant.

Experimental aphids

Branches with winged *A. gossypii* nymphs were collected from the primary host plant, *H. syriacus*, on the campus of Nanjing Agricultural University in April. The collected branches were cultivated in bottles of water at room temperature in a laboratory. Upon emergence, all winged adults were removed daily from the branches. Random samples were taken from these field-derived winged adults to test takeoff behaviour, tethered flight capacity and to examine the number of ovarioles in their gonads.

Tethered flight test

The tethered flight capacity of the newly emerged *A. gossypii* was tested in a computer-linked 32 flight-mill system with a design similar to that described in Riley *et al.* (1997). Here, a thin pin was vertically placed and suspended by two magnets in a flight mill unit, and a balance arm (3.8 cm in length) made of thin copper wire was fixed onto the pin. The sternum of the aphid thorax was attached to one end of the balance arm using 502 glue (Guangzhou Baoshenda Chemical Industry Co. Ltd., China). Each test lasted for four hours. Recordings of the distance and time of each flight, as well as the frequency of flights performed per aphid, were registered using a PC computer. Lastly, the cumulative flight duration of an individual over the testing period was used to assess its flight capacity. The frequency distribution of aphids with different cumulative flight durations was analysed.

Gonad dissection

One-day-old newly moulted winged aphids collected from hibiscus branches were dissected in a drop of water under a stereoscopic microscope to examine the number of ovarioles in their gonads. In total, 179 such aphids were used for this purpose.

Observation of take-off behaviour

The takeoff behaviour of winged *A. gossypii* was observed at the age of one, two and three days after attaining adulthood, using apparatus modified from Zhang & Wang (1991) within a screen cage. This apparatus consisted of a small circular island (diameter, 2.5 cm; height, 1.6 cm) and a cylindrical plastic cage (bottom diameter, 8.1 cm; top diameter, 5.5 cm; height, 12.5 cm; angle between cage wall and bottom, 80 degrees). The isolated island was surrounded by a water trough, whilst two 60 W incandescent electric filament lamps were placed above the cage. Eight to ten newly emerged winged aphids were transferred onto the island and covered by the cage. Observation of takeoff behaviour was begun immediately and lasted 20 min. During this observation period, the duration spent in preparing for takeoff was recorded by a digital timer (Joerex® by Mesuca Creations, 1/100 s, Japan). Any aphid that took off upward and touched the wall of the cage was considered to be a migratory individual. The stop position was marked quickly after an individual aphid had touched the wall. At the end of the trial, the distance from the stop position to the bottom of the

cage was measured with a millimetre ruler. According to the distance, the takeoff angle of each aphid was then calculated. Aphids that remained on the island or in the water trough were regarded as sedentary. During the test, constant illumination was maintained and temperature was kept at around 28°.

Selection based on takeoff behaviour

Ninety-six moulted-winged aphids newly emerged from the collected hibiscus braches were randomly chosen and tested for their takeoff behaviour with the apparatus and procedure described above. Twenty-three individuals that showed takeoff behaviour within 20 min were used to initiate the migratory line, whilst 73 individuals that did not takeoff were allocated to the sedentary line. The two categories were reared as separate asexual lineages on cotton seedlings under the same conditions in growth chambers at a L12:D12 photoperiod, 24°C ambient temperature and 70% R.H. In order to diminish the effect of migratory urge on takeoff behaviour, directional selection was imposed on each of the migratory and sedentary lines when they produced more than 100 alatae. This selection was conducted over four consecutive generations or times (because of the generation overlapping) for the migratory lines (named M_1–M_4) and twice for sedentary lines (named S_1 and S_2). In total, 122, 581, 462 and 232 aphids were measured in lines M_1, M_2, M_3 and M_4, respectively, and 60 individuals each for lines S_1 and S_2. A selected line was considered to be a migratory genotype (M) or sedentary genotype (S) when their takeoff angle or sedentary rate became steady, respectively. The M and S lineages were maintained for induction of sexual morphs. In the meantime, another 96 winged aphids, collected randomly from hibiscus branches, were used to maintain a non-selected line to act as a control. This control line was reared on cotton seedlings under the same conditions as the selected lines, and the same testing procedure was applied, with 60–80 aphids tested per different generations or times.

Cross-breeding experiment

Sexual forms from the selected migratory (M) and sedentary (S) genotype aphids were reared on cotton plants under low temperature (20°C) and short photoperiod (L10:D14) conditions in growth chambers, using methods as described by Gong & Zhang (2001). The reared female and male aphids from the M and S lines were paired to allow copulation in groups on cotton plants at 20°C. Eighteen pairs of M♀ × S♂ and 23 pairs of S♀ × M♂ successfully produced 27 and 11 eggs, respectively, after 20 days. These were incubated on cotton plants in a growth chamber at a temperature-photoperiod regime simulating the winter and spring seasons (i.e. temperature gradually decreased from 20°C to 4°C, and then increased to 24°C by 2°C over four days, respectively; and photophase, firstly shortened to 8 h, then lengthened to 10, 12 and 14 h as the temperature increased to 8, 14 and 20°C, respectively). After some three months, the fundatrix aphids hatched, and the rearing conditions were returned to 24°C, L12:D12. Meanwhile, the M and S aphids were maintained parthenogenetically. When winged aphids were produced, the takeoff behaviour of the hybrids and parthenogenetic offspring were tested as described above.
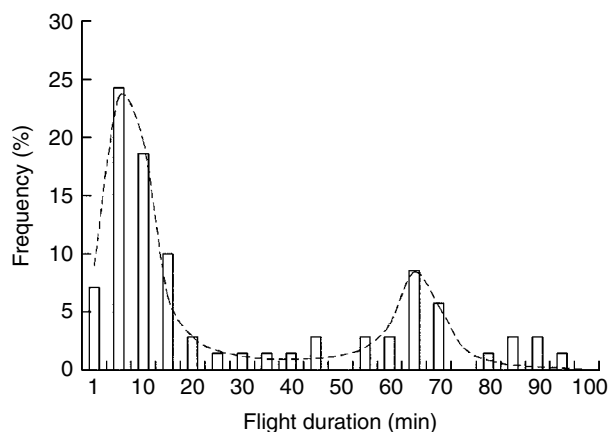

Fig. 1. The distribution frequency of *Aphis gossypii* on the primary host plant with different accumulative flight durations ($n = 70$). The relationship between the frequency (Y) and flight durations (X) can be simulated well by a bimodal curve model, the dashed curve (the model: $Y = (7.199 - 0.226X - 0.00324X^2 - 0.000013X^3)/(1 - 0.244X + 0.0217X^2 - 0.0005X^3 + 0.0000034X^4)$, $r^2 = 0.942$, $F_{7,13} = 30.299$, $P < 0.001$).

Statistical analysis

Differences in takeoff angle, takeoff rate and pre-takeoff time in relation to age, selected generations (times) and genotypes were analysed with ANOVA and followed by multiple comparisons using Tukey method ($P < 0.05$) to separate mean values. The Pearson correlation coefficient was applied to determine the relationship between takeoff angle, takeoff rate and pre-takeoff time. All these statistical analyses were performed using SAS software (SAS Institute Inc., 2001). The frequency distributions of individuals with different flight duration or ovarioles was analysed by a curve estimation method, using the 'curve-fit all equations' process of the TableCurve 2D 5.0 software system (SPSS Inc., 2000), whilst the goodness-of-fit to a curve was tested by ANOVA (F-statistic, $P < 0.05$) along with the correlation of determination (r^2). The curve equation with maximum r^2 value and which passed the F-statistic test was accepted. The forms of the accepted curves were outlined in fig. 1 and fig. 2, and both of them exhibited two peaks.

Results

Population differentiation

In the field, a small proportion of *A. gossypii* remained on the primary host plant, hibiscus, in Nanjing, China, over the summer seasons of 2003, 2004 and 2006 (fig. 3), although a large proportion of this population migrated to secondary hosts. The tree-dwelling aphids existed permanently throughout the year. The result strongly suggests that there may be intra-population differentiation in migratory behaviour in *A. gossypii* and that the host-specific tree-dwelling aphids show a generally poor migratory capacity whereas the host-alternative aphids show a strong such capacity.

The cumulative flight duration in the newly emerged, tethered aphids revealed significant variation within the spring population taken from the primary host plant. The
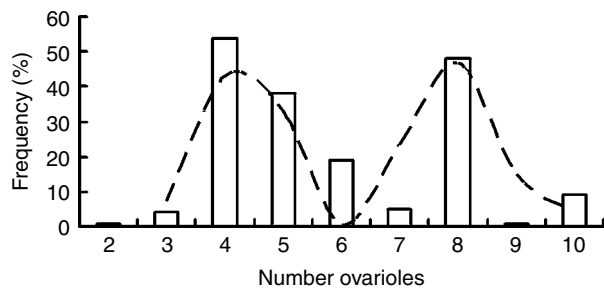
Fig. 2. The frequency distribution of *Aphis gossypii* on the primary host plant with different numbers of ovarioles in their gonads ($n = 179$). The bimodal mode between the frequency (Y) and number of ovarioles (X) is exhibited by the dashed curve (the model: $Y = 26.23 * \sin^2(2\pi X/7.13 + 0.892)$, $r^2 = 0.681$, $F_{6,2} = 6.412$, $P = 0.0324$)
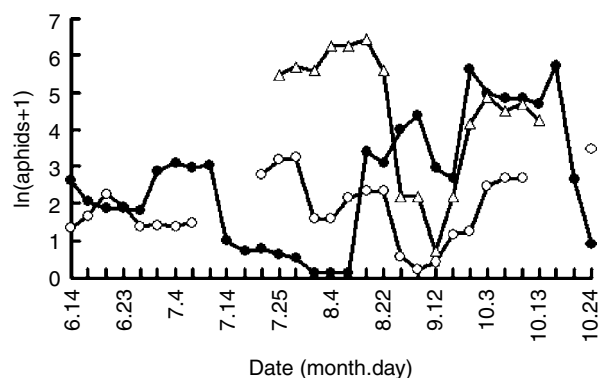

Fig. 3. The population dynamics of *Aphis gossypii* on the 20 cm branch of hibiscus trees (a primary host plant) in 2003, −○−; 2004, −●− and 2006, −△−. There was no investigation from 11 to 18 July in 2003.

frequency of aphids with different flight durations displayed a bimodal distribution, which could be simulated well by a bimodal curve equation ($r^2 = 0.942$, $F_{7,13} = 30.299$, $P < 0.001$; fig. 1). The first peak represents the short-flying phenotype with flight durations of $< \sim 30$ min, whilst the second peak corresponds to the long-flying phenotype with flight durations of > 30 min.

The number of ovarioles in one-day-old post-moulting winged aphids from the primary host plant in spring ranged from two to ten (fig. 2). Of the 179 aphids tested, $\sim 65\%$ possessed less than seven ovarioles in their gonads, whilst $\sim 35\%$ aphids had more than seven ovarioles, displaying a weak bimodal distribution in the frequency of aphids with different numbers of ovarioles ($r^2 = 0.681$, $F_{2,6} = 6.412$, $P = 0.0324$; fig. 2).

The takeoff behaviour was related to the age of these individuals (table 1). There were significant differences in takeoff angle, takeoff rate and pre-takeoff time between one-, two- and three-day-old post-moulting winged aphids (takeoff angle: $F_{2,225} = 15.11$, $P < 0.001$; takeoff rate: $F_{2,82} = 5.13$, $P < 0.01$; pre-takeoff time: $F_{2,225} = 2.87$, $P = 0.05$). The one-day-old aphids took off more readily and at a steeper angle, with a significantly higher takeoff rate, as compared to three-day-old individuals. Therefore, the one-day-old alate

Table 1. The takeoff angle, takeoff rate and pre-takeoff time of *Aphis gossypii* at different post-emergence ages.

Adult age	Takeoff angle (degree)	Takeoff rate (%)	Pre-takeoff time (min)
One day old	59.2 ± 1.8 a	34.8 ± 1.8 a	3.4 ± 0.3 b
Two days old	46.0 ± 2.8 b	41.1 ± 2.3 a	4.0 ± 0.4 ab
Three days old	34.2 ± 3.0 b	17.0 ± 1.9 b	5.4 ± 0.4 a

Means are presented with their standard errors ($\pm$SE). Means within columns followed by different letter(s) are significantly different ($P < 0.05$).

aphids were suitable for screening the migratory and sedentary genotype populations.

Response to selection based on take off behaviour

A. gossypii population showed significant response to selection on takeoff behaviour (table 2). In the migratory line, the average takeoff angle significantly enlarged in response to selection ($F_{4,428} = 13.199$, $P < 0.001$). It increased from 39.8 ± 4.2 degrees in the base population to 68.7 ± 1.9 degrees after four generations (times) of selection, whilst average takeoff angle in the unselected line (control) varied little over generations (times) and was not significantly different ($F_{4,74} = 0.525$, $P = 0.718$). After two rounds of selection, the takeoff angle of migratory line M_2 reached and persisted at about $60°$, whilst there was no significant difference between M_2 and M_4 (table 2). Therefore, these individuals with takeoff angles of around $60°$ may indeed be considered as the migratory genotype. On the other hand, the correlated responses in the takeoff rate and pre-takeoff times were not very strong and regular over the four rounds of selection, although there were significant differences among different times ($F_{4,134} = 4.040$, $P = 0.004$ in takeoff rate; $F_{4,428} = 16.421$, $P < 0.001$ in pre-takeoff time). In fact, there was no significant correlation of takeoff angle with takeoff rate ($r = 0.582$, df = 4, $P = 0.303$) or with pre-takeoff time ($r = 0.267$, df = 4, $P = 0.664$). In contrast, selection against take-off behaviour significantly altered the takeoff rate in the sedentary line compared to the base population ($F_{2,12} = 3.892$, $P = 0.05$), decreasing from $16.8 \pm 8.1\%$ in the base population to $12.4 \pm 10.4\%$ in S_1 and $3.5 \pm 9.0\%$ in S_2, whilst there was no significant difference between S_1 and S_2 (fig. 4). Therefore, we consider the virtually 'non-takeoff' individuals from S_2 as the sedentary genotype.

Inheritance of takeoff behaviour

There were significant differences in takeoff angle and takeoff rate among the hybrid offspring and the asexual parental lineages ($F_{3,214} = 3.154$, $P < 0.05$ in takeoff angle; $F_{3,64} = 8.432$, $P < 0.001$ in takeoff rate) (table 3). Takeoff rate in the hybrid offspring was significantly higher than that in the migratory phenotype (M) and sedentary phenotype (S), being ranked as $M♀ \times S♂ = S♀ \times M♂ > M > S$. The takeoff rate had no maternal effect in the inheritance. The average takeoff angle was ranked as $M♀ \times S♂ > S♀ \times M♂ > M > S$, though only the hybrid offspring from $M♀ \times S♂$ could be statistically separated from the sedentary phenotype. If the takeoff angle of aphids that did not perform takeoff behaviour was considered as zero, the takeoff angles of the

Table 2. The takeoff angle, takeoff rate and pre-takeoff time of *Aphis gossypii* in the migratory line of four times of selection.

Selected population[1]	Takeoff angle (degree)		Takeoff rate (%)	Pre-takeoff time (min)
	Selected population	Non-selected population		
M_0	39.8 ± 4.2 c	39.8 ± 4.2 a	16.8 ± 1.7 b	5.1 ± 0.8 cd
M_1	48.1 ± 2.5 c	39.8 ± 2.9 a	25.6 ± 1.8 ab	6.8 ± 0.6 ab
M_2	60.6 ± 1.5 ab	45.3 ± 3.5 a	34.5 ± 1.4 a	3.6 ± 0.2 d
M_3	55.3 ± 2.4 b	36.0 ± 3.7 a	23.6 ± 1.5 ab	5.6 ± 0.5 bc
M_4	68.7 ± 1.9 a	38.2 ± 3.4 a	24.7 ± 1.8 ab	7.8 ± 0.7 a

Means are presented with their standard errors (±SE). Means within columns followed by different letter(s) are significantly different ($P < 0.05$).
[1] M_0, the original population for selection; M_1–M_4, the population selected for 1–4 times, respectively.
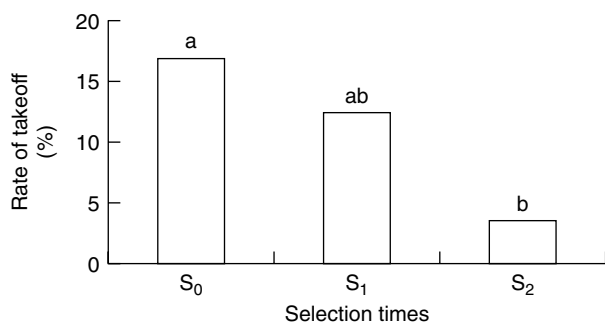

Fig. 4. Change in takeoff rate of the sedentary line due to negative selection on takeoff behaviour. Means labelled with the same letter(s) are not significantly different ($P > 0.05$).

Table 3. Takeoff angle and takeoff rate in hybrid offspring as well as migratory (M) and sedentary (S) genotype of *Aphis gossypii*.

Treatment	Takeoff angle (degree)[1]	Takeoff angle (degree)[2]	Takeoff ratio (%)
M♀ × S♂	61.5 ± 2.7 a	30.7 ± 3.3 a	48.1 ± 6.2 a
S♀ × M♂	56.3 ± 2.5 ab	19.5 ± 2.2 b	37.2 ± 6.5 a
M[3]	54.4 ± 2.9 abc	15.8 ± 2.2 b	34.4 ± 2.2 ab
S[3]	50.5 ± 2.2 bc	10.5 ± 1.3 c	21.6 ± 2.1 b

Means (±SE) within columns followed by different letter(s) are significantly different ($P < 0.05$).
[1] Mean takeoff angle of all the aphids that performed takeoff.
[2] Mean takeoff angle of all tested aphids in which the angle of the non-takeoff aphid was considered as zero.
[3] Asexual parents.

hybrid offspring and the asexual parental lineages were significantly different ($F_{3,715} = 15.251$, $P < 0.001$), and ranked as M♀ × S♂ > S♀ × M♂ = M > S. These results indicate the presence of a maternal effect in the inheritance of takeoff angle.

Discussion

As outlined in the introduction, the cotton-melon aphid, *A. gossypii*, is known to be a holocyclic species exhibiting host alternation, overwintering in the egg stage on a woody host and propagating parthenogenetically on various herbaceous secondary hosts in the summer (Blackman & Eastop, 1984, 1994; Ding & Su, 2002). However, as this study has demonstrated, in the Yangtze River Valley of China, a small proportion of the population remains on the primary host plant (hibiscus trees) throughout the summer period. The fact that not all the aphids overwintering on hibiscus leave the primary host plant and emigrate to the secondary hosts reveals the presence of two phenotypes, host-specific and host-alternating, in the same spring population. A similar phenomenon was observed for *A. gossypii* in northern Italy by Ferrari & Nicoli (1994). It is also known in the case of the damson-hop aphid, *Phorodon humuli* (Schrank), in the UK and in the USA on its primary host, *Prunus* spp., especially *P. spinosa* (Wright *et al.*, 1995; Loxdale *et al.*, 1998). The coexistence of two types of life-history in *A. gossypii* populations may have resulted from weather conditions selecting for population genetic differentiation in flight capacity.

Weather conditions influence the takeoff behaviour and migratory flight of insects, especially small ones; for example, an increase in wind speed can delay or decrease the takeoff incident of aphids (Walters & Dixon, 1984) and whiteflies (Rufus *et al.*, 1999). In Nanjing, China, the emergence peak of alate *A. gossypii* on the primary host occurs at around 21:00 h, and the migration peak of aphids usually occurs at midday (Dixon, 1998; Liu *et al.*, 2003b). Additionally, the one- or two-day-old post-moulting winged aphids are able to perform the larger takeoff angle and stronger migratory urge (table 1), so suitable weather conditions prevailing during 15 h and 39 h after adult emergence are vital for the occurrence of migration in this aphid species. If rainy or windy weather occurs during the migratory period, the winged aphids are forced to cease migrating and produce offspring on the primary host plant instead. The offspring of these may, in turn, become the source of aphids on hibiscus trees over the summer season. However, weather conditions alone are not capable of explaining the phenomena observed in Italy over the period 1992–1993 (Ferrari & Nicoli, 1994) nor in China from 2003–2006.

Intra-population differentiation in migratory behaviour may explain the coexistence of host-specific and host-alternating life cycles in *A. gossypii*, as in other biological characters observed in different aphid species (Sunnucks *et al.*, 1997, 1998; Fuller *et al.*, 1999). The spring populations on hibiscus are likely to differentiate into migratory and sedentary genotypes in the Yangtze River Valley of China. The migratory aphids will leave hibiscus when the quality of

the primary host deteriorates and the climate becomes hot, whilst the sedentary ones remain on the tree because of low takeoff tendency and poor flight capacity. There is substantial variation in flight capacity and the number of ovarioles in the gonads of *A. gossypii* (figs 1 and 2). Our previous studies suggested the presence of an oogenesis-flight syndrome in the population of *A. gossypii*, since significantly fewer ovarioles were found in the winged aphids caught at a height of 20 m above ground than in those collected from the primary host (Liu *et al.*, 2003a,b). Thus, empirical data obtained from both previous studies, as well as the present one, support the hypothesis of differentiation in migratory behaviour within the spring population of this aphid species. Similar phenomena have been found previously, including by Kidd and Cleaver (1984, 1986) in the black bean aphid, *Aphis fabae* Scopoli, and by Blackmer *et al.* (1995) in whitefly, *Bemisia tabaci* (Hemiptera: Aleyrodidae). In *A. fabae*, some alate asexules reproduce before taking off ('flyers') while others do not ('migrants'), and the migrants have an innately greater urge to take off than flyers (Kidd & Cleaver, 1984, 1986). In whitefly populations, there are long- and short-distance flyers, and settled individuals, and these exhibit behavioural, morphological and physiological differences (Blackmer & Byme, 1993; Blackmer *et al.*, 1995).

The present study provides further evidence that the intra-population variability of migratory behaviour in *A. gossypii* is of genetic origin, since the population displayed significant response to bidirectional selection on takeoff behaviour. The individual aphids with larger takeoff angles are presumably more likely to reproduce winged offspring than those with smaller takeoff angles, so that a greater part of the population of winged offspring would derive from the aphids performing larger takeoff angles in selection experiments. As such, the average takeoff angle of the offspring population was enlarged after successive rounds of selection. Indeed, our previous study demonstrated that the migratory line produces winged offspring more readily than the sedentary line (Liu *et al.*, 2006).

The results of reciprocal crossing between sexual forms of the migratory and sedentary genotypes confirm the genetic control of takeoff behaviour in *A. gossypii*. Interestingly, takeoff angle of the hybrids from the cross M♀ × S♂ was significantly larger than that of the offspring from the cross S♀ × M♂, suggesting inheritance of takeoff angle involves a maternal effect, as for a migratory trait in the cowpea weevil, *Callosobruchus maculatus* (F.) (Coleoptera: Chrysomelidae) (Messina, 1987), and wing morphs in brown planthopper, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) (Wang *et al.*, 1997). Although the takeoff rate was also heritable, it did not show any sex-linkage and maternal effect, since takeoff rate was compatible between offspring from the crosses M♀ × S♂ and S♀ × M♂.

The genetically based intra-population differentiation might be of adaptive significance and, hence, reflect an evolutionary consequence in *A. gossypii*, as in other hetero-ecious species (Sunnucks *et al.*, 1997, 1998; Fuller *et al.*, 1999). Long-distance, host-orientated migration in aphids has the risk of starvation and even death (Dixon, 1998; see also Loxdale *et al.*, 1993; Loxdale & Lushai, 1999). Some *A. gossypii* individuals always remained settled on the primary host hibiscus, whereas a great part of the spring population migrates in order to find summer host plants both in northern Italy (Ferrari & Nicoli, 1994) and the Yangtze River Valley. Our findings suggest that the presence of *A. gossypii*

individuals (genotypes) remaining on the primary host over the summer season is not accidental; rather, it is an evolved strategy for ecological adaptation to variable environmental conditions.

References

Blackmer, J.L. & Byme, D.N. (1993) Flight behaviour of *Bemisia tabaci* in a vertical flight chamber: Effect of time of day, sex, age and host quality. *Physiological Entomology* **18**, 223–232.

Blackmer, J.L., Byrne, D.N. & Tu, Z. (1995) Behavioural, morphological, and physiological traits associated with migratory *Bemisia tabaci* (Homoptera: Aleyrodidae). *Journal of Insect Behavior* **8**, 251–267.

Blackman, R.L. & Eastop, V.F. (1984) *Aphids on the World's Crops: An Identification and Information Guide*. 466 pp. Chichester, UK, John Wiley.

Blackman, R.L. & Eastop, V.F. (1994) *Aphids on the World's Trees*. 987 pp. Wallingford, UK, CAB International.

Byrne, D.N., Buchmann, S.L. & Spangler, H.G. (1988) Relationship between wing loading, wing beat frequency and body mass in homopterous insects. *Journal of Experimental Biology* **135**, 9–23.

Ding, J.H. & Su, J.Y. (2002) *Agricultural Entomology*. pp. 242–244. Beijing, Agricultural Press of China.

Dixon, A.F.G. (1998) *Aphid Ecology*. 2nd edn. pp. 128–186. London, Chapman & Hall.

Ferrari, R. & Nicoli, G. (1994) Life cycle and natural enemies of *Aphis gossypii* Glover: first observations. *Informatore Fitopatologico* **44**, 59–62.

Fuller, S.J., Chavigny, P., Lapchin, L. & Valerberghe-Masutti, F. (1999) Variation in clonal diversity in glasshouse infestations of the aphid, *Aphis gossypii* Glover, in southern France. *Molecular Ecology* **8**, 1867–1877.

Gatehouse, A.G. (1997) Behaviour and ecological genetics of wind-borne migration by insects. *Annual Review of Entomology* **42**, 475–502.

Gong, P. & Zhang, X.X. (2001) The inducement of temperature and photoperiod to produce sexuals of *Aphis gossypii* Glover. *Acta Phytophylacica Sinica* **28**, 318–324.

Isard, S.A., Irwin, M.E. & Hollinger, S.E. (1990) Vertical distribution of aphids (Homoptera: Aphididae) in the planetary boundary layer. *Environmental Entomology* **19**, 1473–1484.

Kidd, N.A.C. & Cleaver, A.M. (1984) The relationship between pre-flight reproduction and migratory urge in alatae of *Aphis fabae* Scopoli (Hemiptera: Aphididae). *Bulletin of Entomological Research* **74**, 517–527.

Kidd, N.A.C. & Cleaver, A.M. (1986) The control of migratory urge in *Aphis fabae* Scopoli (Hemiptera: Aphididae). *Bulletin of Entomological Research* **76**, 77–87.

Liu, X.D., Zhai, B.P., Zhang, X.X. & Xiong, F. (2003a) The relationship between flight behaviour and ovary

development in *Aphis gossypii* Glover. *Entomological Knowledge* **40**, 39–42.

Liu, X.D., Zhang, X.X. & Zhai, B.P. (2003b) Flight activity rhythm of *Aphis gossypii* Glover in Nanjing and its flight capacity. *Acta Entomologica Sinica* **46**, 489–493.

Liu, X.D., Zhai, B.P., Liang, S.A., Xu, X.H. & Gong, Q.H. (2006) Migratory and sedentary strains of *Aphis gossypii* Glover and the flight characteristics of their hybridized offspring. *Acta Entomologica Sinica* **49**, 619–624.

Loxdale, H.D. & Lushai, G. (1999) Slaves of the environment: the movement of insects in relation to their ecology and genotype. *Philosophical Transactions of the Royal Society of London Series B: Biological Science* **354**, 1479–1495.

Loxdale, H.D., Hardie, J., Halbert, S., Foottit, R., Kidd, N.A.C. & Carter, C.I. (1993) The relative importance of short- and long-range movement of flying aphids. *Biological Reviews* **68**, 291–311.

Loxdale, H.D., Brookes, C.P., Wynne, I.R. & Clark, S.J. (1998) Genetic variability within and between English populations of the damson-hop aphid, *Phorodon humuli* (Hemiptera: Aphididae), with special reference to esterases associated with insecticide resistance. *Bulletin of Entomological Research* **88**, 513–526.

Messina, F.J. (1987) Genetic contribution to the dispersal polymorphism of the cowpea weevil (Coleoptera: Bruchidae). *Annual Entomology Society of American* **80**, 12–16.

Reynolds, D.R., Mukhopadhyay, S., Riley, J.R., Das, B.K., Nath, P.S. & Mandal, S.K. (1999) Seasonal variation in the windborne movement of insect pests over northeast India. *International Journal of Pest Management* **45**, 195–205.

Riley, J.R., Downham, M.C.A. & Cooter, R.J. (1997) Comparison of the performance of *Cicadulina* leafhoppers on flight mills with that to be expected in free flight. *Entomologia Experimentalis et Applicata* **83**, 317–322.

Rufus, I., Willis, M. & Byrne, D. (1999) Modulation of whitefly takeoff and flight orientation by wind speed and visual cues. *Physiological Entomology* **24**, 311–318.

SAS Institute Inc. (2001) JMP user's guide, ver. 4. Cary, NC, USA, SAS Institute Inc.

SPSS Inc. (2000) TableCurve 2D 5.0 for Windows. Chicago, IL, USA, SPSS Inc.

Sunnucks, P., De Barro, J., Lushai, G., Maclean, N. & Hales, D. (1997) Genetic structure of an aphid studied using microsatellites: cyclic parthenogenesis, differentiated lines and host specialization. *Molecular Ecology* **6**, 1059–1073.

Sunnucks, P., Chisholm, D., Turak, E. & Hales, D. (1998) Evolution of an ecological trait in parthenogenetic *Sitobion* aphids. *Heredity*, **81**, 638–647.

Taylor, L.R., Woiwod, I.P. & Taylor, R.A.J. (1979) The migratory ambit of the hop aphid and its significance in aphid population dynamics. *Journal of Animal Ecology* **48**, 955–972.

Walters, K.F.A. & Dixon, A.F.G. (1983) Migratory urge and reproductive investment in aphids: variation within clones. *Oecologia* **58**, 70–75.

Walters, K.F.A. & Dixon, A.F.G. (1984) The effect of temperature and wind on the flight activity of cereal aphids. *Annals of Applied Biology* **104**, 17–26.

Wang, Q., Du, J.G. & Cheng, X.N. (1997) Genetics studies on wing dimorphism of brown planthopper, *Nilaparvata lugens* (Homoptera: Delphacidae). *Acta Entomologica Sinica* **40**, 343–348.

Wright, L.C., Pike, K.S., Allison, D. & Cone, W.W. (1995) Seasonal occurrence of alate hop aphids (Homoptera, Aphididae) in Washington-state. *Journal of Agricultural Entomology* **12**, 9–20.

Zhang, X.X. & Wang, M.T. (1991) Studies on the relationship between variation of ovary canal number and the takeoff behaviour in green peach aphid. *Acta Phytophylacica Sinica* **18**, 161–166.