# FLIGHT IN THE VETCH APHID, *MEGOURA VICIAE* BUCKTON

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# 1. INTRODUCTION

Many aphid species, which occur as parthenogenetic viviparous morphs in the spring and summer, react to adverse changes in the environment by producing alate virginoparae which fly away and colonise new hosts. Aspects of the environment which have been shown to herald poor environmental conditions and to cause alate individuals to be produced are changes in temperature ( Wadley, 1923; Ewing, 1926; Shull, 1929; White 1946; Kenten, 1955; Johnson, 1966a; Lamb & White, 1966 ) and photoperiod ( Shull, 1928, 1929; White, 1946; Kitzmiller, 1950; Kenten, 1955; Buckle, 1963a,b(in Hille Ris Lambers, 1966); MacGillivray & Anderson, 1964; Johnson, 1965, 1966b ), crowding ( Wadley, 1923; Reinhard, 1927; Bonnemaison, 1949, 1950, 1951; Noda, 1958; Lees, 1961; Lowe & Taylor, 1964; Toba et al, 1967; Sutherland, 1969; Shaw, 1970a) and nutrition ( Schaefer, 1938; Wilson, 1938; Noda, 1956, 1958; Johnson & Birks, 1960; Johnson, 1966b; Branson & Simpson, 1966; Sutherland, 1967; Lees, 1966 ). The effects of nutrition are usually difficult to separate from those of crowding since a large population of aphids will lower the quality of the host plant.

Crowding acts as a stimulus in various ways and to different degrees in different aphid species. In Megoura viciae ( Buckton ) ( Lees, 1961 ) and Acyrthosiphon pisum ( Harris ) ( Sutherland, 1969 ) crowding of the mother only is important whereas in Aphis craccivora ( Koch ) ( Johnson, 1965 ), Myzus persicae ( Awram, 1968 ), Aphis

fabae ( Scop. ) ( Shaw, 1970a), Chaetosiphon fragifoliae ( Cockerell ) ( Judge &. Schaefers, 1971), Macrosiphum granarium (Noda, 1961) and Rhopalosiphum padi ( L. ) ( Dixon & Glen, 1971 ) both pre- and post-natal crowding influence the proportion of alatae produced. Rhopalosiphum prunifoliae ( Noda, 1958 ) and Therioaphis maculata ( Buckton ) ( Toba et al, 1967 ) are responsive to crowding purely post-natally and then only during the first eighteen hours after birth.

The situation so far studied for Brevicoryne brassicae ( L. ) is very confused. Bonnemaison ( 1951 ) found that for alatae to be produced mother and offspring had to be reared together; in other words, some form of mutual stimulation occurs. Kawada ( 1964 ) subsequently found that when larvae were reared in crowds without the mother from first instar to the adult stage more became alate than when they were reared in isolation, although quality of the host plant may have played a part. Lamb and White ( 1966 ), however, found that B. brassicae crowded for periods of up to twenty four hours produced no more alate larvae than those reared in isolation.

Quality of the food plant has been invoked as a major cause of the production of alate morphs. Starvation was thought to be the reason for increased numbers of alatae in A. pisum ( Schaefer, 1938 ). Pintera ( 1957 ) working with M. persicae and Johnson ( 1966a ) with A. craccivora came to similar conclusions. However, the most

important nutritional factor, first suggested by Evans ( 1938 ) working on B. brassicae, seems to be variation in the amount of amino-nitrogen. When young Dysaphis devecta were reared on plants given a nitrogen deficient diet for the first four days of life a large proportion became alate ( Forrest, 1970 ). Mature plant tissue contains less amino-nitrogen than young or senescing tissue and it is on mature tissue that higher numbers of alatae tend to be produced ( Pintera, 1957; Johnson, 1966b; Sutherland, 1969 ). Laboratory studies involving rearing Myzus persicae on synthetic diets appear to contradict the results obtained using whole plant diets. Deficiencies in amino acids and sucrose in the maternal diet gave rise to a greater proportion of apterae amongst the offspring ( Mittler & Kleinjan, 1970 ). Artificial diets, however, may lack substances essential for alata production which occur in whole plants but which have not yet been identified. R. padi reared in isolation on maturing bird cherry produced smaller offspring in successive generations ( Dixon & Glen, 1971 ).

Alata production is induced in many species by low temperatures ( White, 1946; Noda, 1954; Johnson & Birks, 1960; Lamb & White, 1966; Lees, 1967 ). Often the effect of temperature is interrelated with some other factor e.g. nature of the host ( Noda, 1954 ) as in R. prunifoliae, photoperiod as in A. craccivora ( Johnson, 1965 ). Both photoperiod and temperature can affect the threshold of response to other stimuli ( Johnson, 1966a).

Alatae have been described as obligatory migrants differing

physiologically and behaviourally as well as structurally from the apterous morph of the same species. Some migratory insect species produce winged interforms, which do not have complete wings or wing muscles. Aphid species produce these intermediates which range from apterous individuals with alata-like sclerotisation of the thorax and abdomen to alatae with one wing shorter than another or with miniature wings ( Lees, 1966 ).

In many insects migration occurs in young individuals before the ovaries are mature. This connection between migratory behaviour and pre-oviposition stages was first pointed out as a result of work on locusts and aphids ( Kennedy, 1956, 1961; Johnson, 1963 ). It has been suggested that in migratory individuals sensori-motor functions are developed at the expense of vegetative functions i.e. settling, feeding and larviposition ( Kennedy, 1958, 1961 ). This antagonistic development of sensori-motor and vegetative functions has been called the "oogenesis-flight syndrome" ( Johnson, 1963, 1969 ).

Environmental conditions are thought to act on an aphid during its development favouring one or other of two antagonistic systems, the first promoting migration by the development of flight muscles and the build-up of fat and glycogen reserves and the second promoting the vegetative functions of settling, feeding and larviposition ( Kennedy, 1961 ). When an insect becomes adult its structural development has already determined whether it will

migrate or not. It has been suggested, however, that the oogenesis-flight syndrome is more a measure of the aphid's ability to fly when gravid than a measure of migratory capacity ( Dixon, 1971 ).

It was suggested that a polymorphism of behaviour and physiology as well as of structure might occur in aphids ( Johnson, 1963 ). Recent work on A. fabae has given more weight to the ontogenetic theory of flight behaviour. Different degrees of expression of migratory urge are seen among alatae of A. fabae. In a young colony large alatae are produced. These are mainly "fliers" which deposit some larvae before they fly and "non-fliers" which never fly. However, no attempt was made to make "non-fliers" fly. As the colony grows the alatae produced become smaller, have a slighter wing loading and fly without depositing larvae. These "migrants" diminish in numbers as the colony nears the end of its life and "fliers" and "non-fliers" again predominate ( Shaw, 1970b, c ).

The ontogenetic theory allows no behavioural choice for an aphid which is alate because of conditions experienced by its mother or during its early life, and which suddenly finds itself in a favourable environment. A situation where an alata spends its larval life in a favourable environment which later becomes unfavourable must also frequently arise. In species where alate characters are influenced by conditions during larval life intermediates, which cannot fly, will arise as in A. fabae ( Shaw, 1970c ). However, in species where alata determination occurs

before birth, the situation is very different because all alatae will be structurally capable of flight when they moult to adult. Any behavioural intermediacy could not be associated with differences in wing loading, amount of wing muscle or the quantity of fuel stored as fat.

To test whether an ontogenetic theory can explain the flight behaviour of aphids the vetch aphid, Megoura viciae ( Buckton ) was used. In this aphid alata determination occurs before birth ( Lees, 1967 ).

## 2. MATERIALS AND METHODS.

A parthenogenetic clone of Megoura viciae, brought from Rothamsted Experimental Station in 1968, was maintained as a parthenogenetic clone for use in the experiments described here.

The aphids were reared on seedlings of broad bean, Vicia faba ( L. ) var. Kerr's Exhibition Longpod. Beans were soaked for 24 hours and then placed between layers of damp cotton wool to germinate. Five or six days later, when the seedlings were at the "hook stage", they were planted in John Innes No. 1 Potting Compost in $4\frac{1}{2}$" plant pots. About eight days after germination the seedlings were ready for use as host plants.

Aphids were reared indoors under constant conditions. A daily regime of 17 hours light and 7 hours darkness with temperatures of 20°C during the light period and 15°C during the dark period, giving a daily average of 18.5°C, was maintained throughout all experiments.

The walls and ceiling of the room were lined with reflecting foil. 80 Watt daylight and white fluorescent lights gave a light intensity of 3660 metre candles ( 340 foot candles ) at bench level.

Relative humidity remained at appriximately 70%.

Handling aphids.

First and second instar larvae were transferred from one plant to another by means of a camel hair brush. Older larvae and adults were removed from one host by shaking or tapping the plant so that they would fall into a specimen tube. These were allowed to crawl on to a new host without interference from the experimenter. This latter method is thought to be unlikely to interfere with the subsequent behaviour of the animals since the avoidance behaviour and struggling, which usually arise when the larger larvae and adults are picked up with a camel hair brush, do not occur.

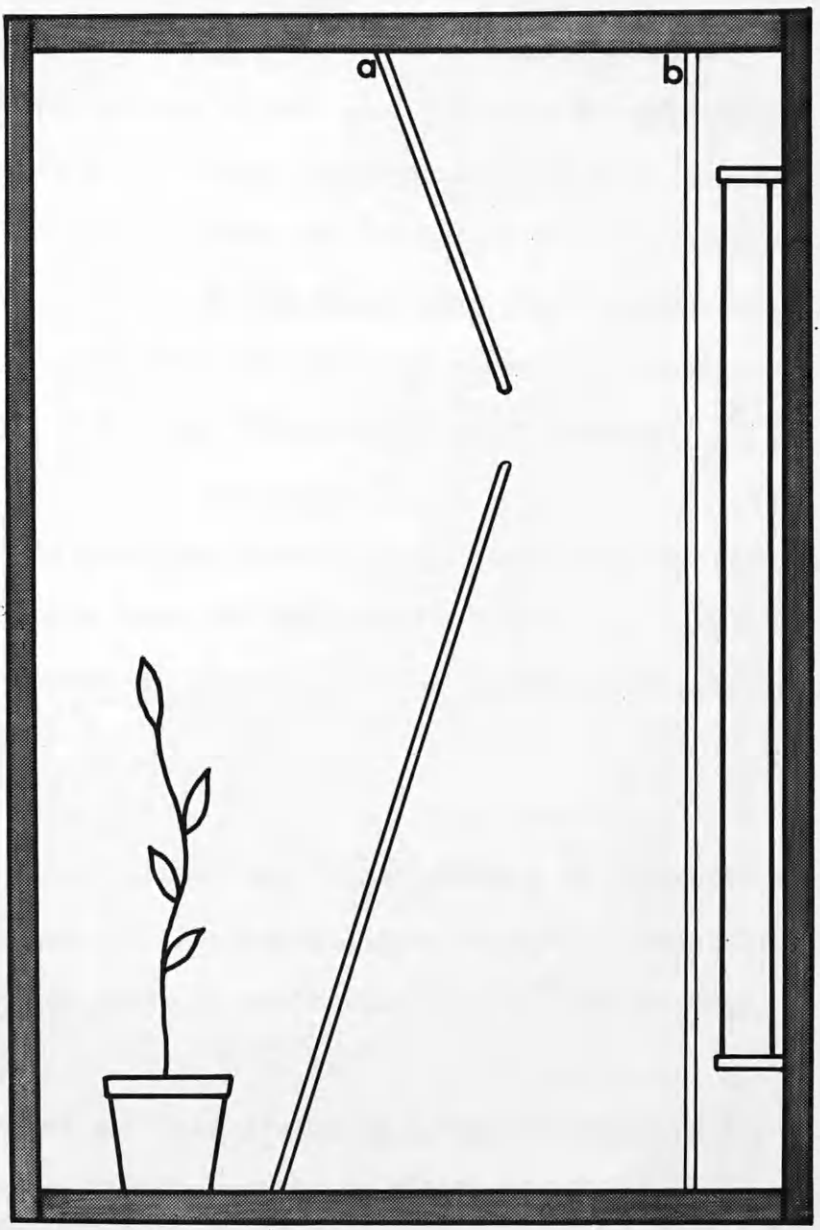
Production of alatae.

To obtain regular quantities of alate virginoparae adult apterae were crowded using Lees' ( 1961 ) method. 10 apterae were crowded for 24 hours in a 2.5 x 5 cm specimen tube containing a piece of moist filter paper. Afterwards they were returned singly to bean seedlings to reproduce. Alatae were then produced.

Flight cabinet.

When alatae moulted to adult the host plants with the aphids were placed in the black painted chamber of the flight cabinet

Figure 1. Flight cabinet (Dixon, 1969).


a
b
Black chamber
White chamber
Fluorescent light chamber

shown in Figure 1 ( Dixon, 1969 ).

Alatae taking off from the plant are attracted by the fluorescent lights and fly towards the sloping sheets of glass ( a in Figure 1 ). They alight on the glass, crawl towards the gap between the plates and either fly or crawl into the white middle chamber. Once inside the middle chamber they do not return to the host plant. By means of small doors at either end of the white chamber the flown aphids can be removed from the sheet of glass ( b ) facing the lights or from the ceiling or floor of the white chamber.

When settling after flight is required to take place without interference from the experimenter plants can be placed in the white chamber and removed when an aphid has alighted and begun to feed.

Overheating of the flight cabinet is prevented by circulating air through the fluorescent light chamber by means of a fan in the top and air vents in the bottom of the light chamber.

Plant pots are placed in a tray of water in the black chamber so that any aphid crawling or falling from its plant cannot reach the middle chamber. Any alate aphid found in the middle chamber has therefore flown.

Fliers and non-fliers.

If an alata takes off from the host plant it is a flier, if it remains on the plant it is a non-flier.

Light microscope studies.

Legs, antennae and wings were removed from alate aphids before fixation in Bouin's Fixative. The specimens were embedded in ester wax and cut either in longitudinal or in sagittal sections of 6 μ thickness. They were arranged serially on slides, stained in Mayer's Haemalum and Eosin and mounted in Canada Balsam.

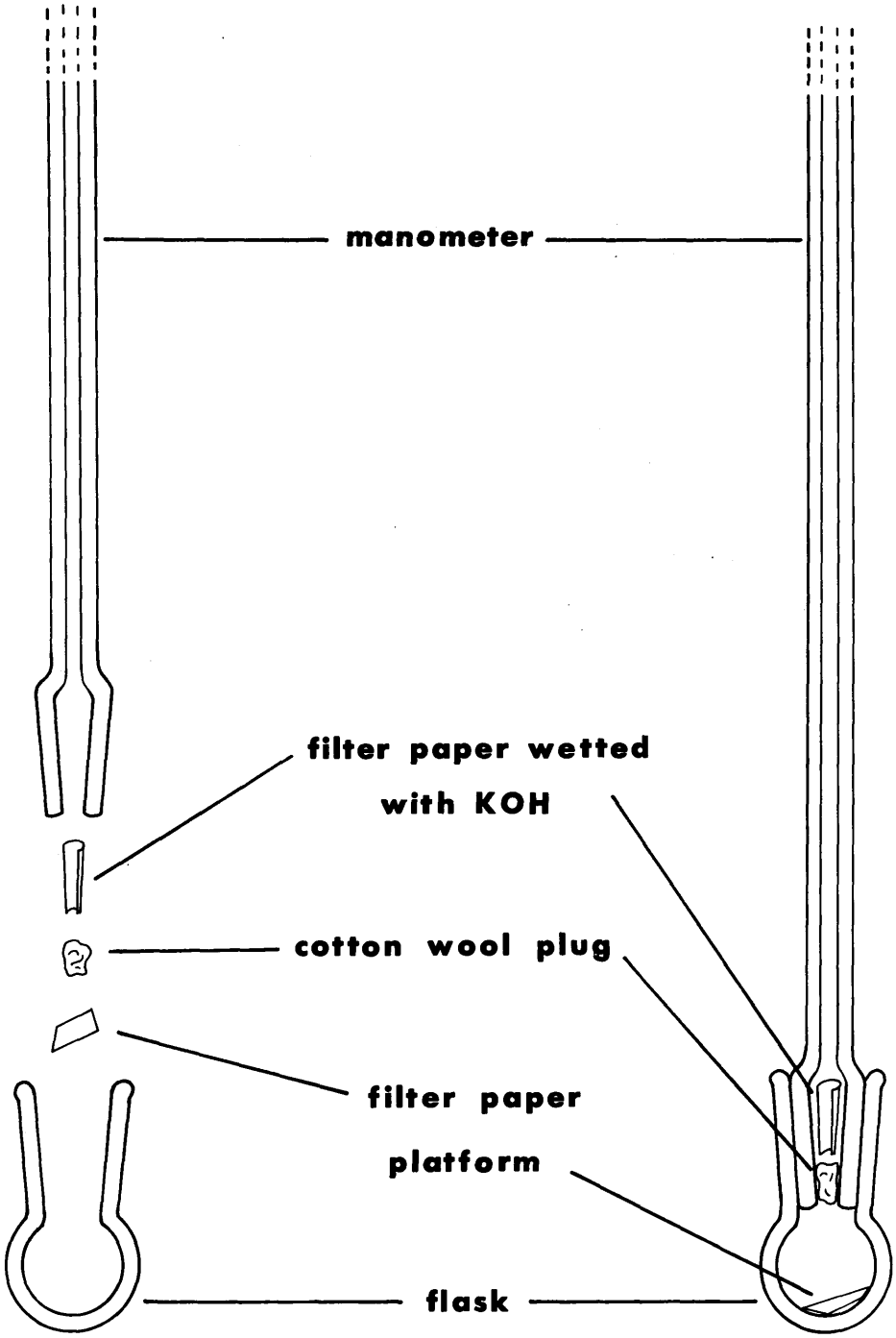
Electron microscope studies.

Whole thoraces of alate aphids, with wings and legs removed, were fixed using a double fixation method with glutaraldehyde and osmium tetroxide in a phosphate buffer, pH 6.8.

In order to locate and orientate the muscle correctly thick sections ( about 1 μ ) were taken on the LKB ultramicrotome and stained with 1% Azur II - Methylene blue ( Richardson, Jarret & Finke, 1960 ).

500Å - 600Å sections were cut on the ultratome, stained with uranyl acetate and lead citrate and viewed on an AEI EM6 Electron

Figure 2. Capillary Respirometer ( after Dixon (1970) ).


manometer
filter paper wetted
with KOH
cotton wool plug
filter paper
platform
flask

Microscope. Cross-sectional areas of mitochondria and muscle fibrils were measured using a planimeter on the resulting micrographs.

Respirometry.

Respiration rates of aphids were measured using the capillary respirometer ( Engelmann, 1963 ). This consists of a manometer made with precision bore glass tubing of .5 mm diameter and a small flask with a volume of .5 ml ( Figure 2 ) in which the aphid is placed. A small piece of filter paper is used to line the flask so that the aphid has a rough surface to grip and will not spend its time struggling.

A number of such flasks and manometers are connected to a large bottle of air and the whole apparatus is kept at the required temperature by immersing it in a water bath. Readings are made directly from a scale behind each manometer. The piece of filter paper in the chamber at the end of the manometer tube is soaked with concentrated KOH solution to absorb $CO_2$ when $O_2$ uptake is being measured.

# RESULTS

## 3(a). FLIGHT BEHAVIOUR

In an earlier experiment it was found that alatae of M. viciae can respond to current adverse conditions. When crowded with other aphids from the fourth instar a much higher proportion of alatae flew on reaching the adult stage than when alatae were isolated from this time ( Dixon, Burns & Wangboonkong, 1968 ).

Further experiments investigating the flight response of alatae of M. viciae to different conditions during larval development and at the time of adult moult are described here.

Temperature, humidity and photoperiod remained constant throughout the experiments ( p.7 ). Nutrition does not affect alata production in M. viciae ( Lees, 1967 ) and so the only differences which could arise between individual alatae, apart from a random variation, would be the result of experience of previous generations. The best cumulative measure of this was thought to be the percentage of alatae among the offspring of the mothers of the experimental alatae. As larvae were isolated during the first one to three days after the crowding treatment the conditions experienced by the mother were unlikely to have varied sufficiently for any great variation to have been imparted to her offspring in this time.

Table 1. Numbers of alatae flying and remaining on the plant when isolated alatae are crowded at 4th instar and just after the adult moult.

| REARING CONDITIONS | FLIERS | NON-FLIERS | TOTAL |
|---|---|---|---|
| Isolated throughout | 1 | 5 | 6 |
| Crowded at 4th instar with 30 3rd instars | 10 | 2 | 12 |
| Crowded after moult with 30 3rd instars | 12 | 3 | 15 |

Apterous virginoparae which had been reared in isolation from birth were given the standard crowding treatment ( p.8 ) and the larvae subsequently produced reared in isolation or in crowds on young bean seedlings. When alatae were crowded after adult moult or during the fourth instar the same proportion flew ( Table 1 ). Since crowding after adult moult had to be done within 12 hours of the moult crowding at fourth instar was more convenient and was used in all subsequent experiments.

Four rearing regimes were used:

(i) isolation from birth until time of flight

(ii) isolation until fourth instar, then crowded on the original plant with a number of third instar nymphs

(iii) crowded rearing from day of birth until time of flight

(iv) crowded rearing until the fourth instar, then isolation on fresh seedlings.

Results of the experiments are given in Tables 1 to 4 in Appendix 1 and in Figures 3 to 7.

The relationships between percentage fliers (Y) and the percentage alate offspring of the mother ($X_1$) and the size of crowd ($X_2$) for the four rearing conditions are represented by equations 1 to 5 below.

Figure 3. Percentage fliers arising when alatae are isolated from birth until time of flight plotted against the percentage alate progeny of the mother.

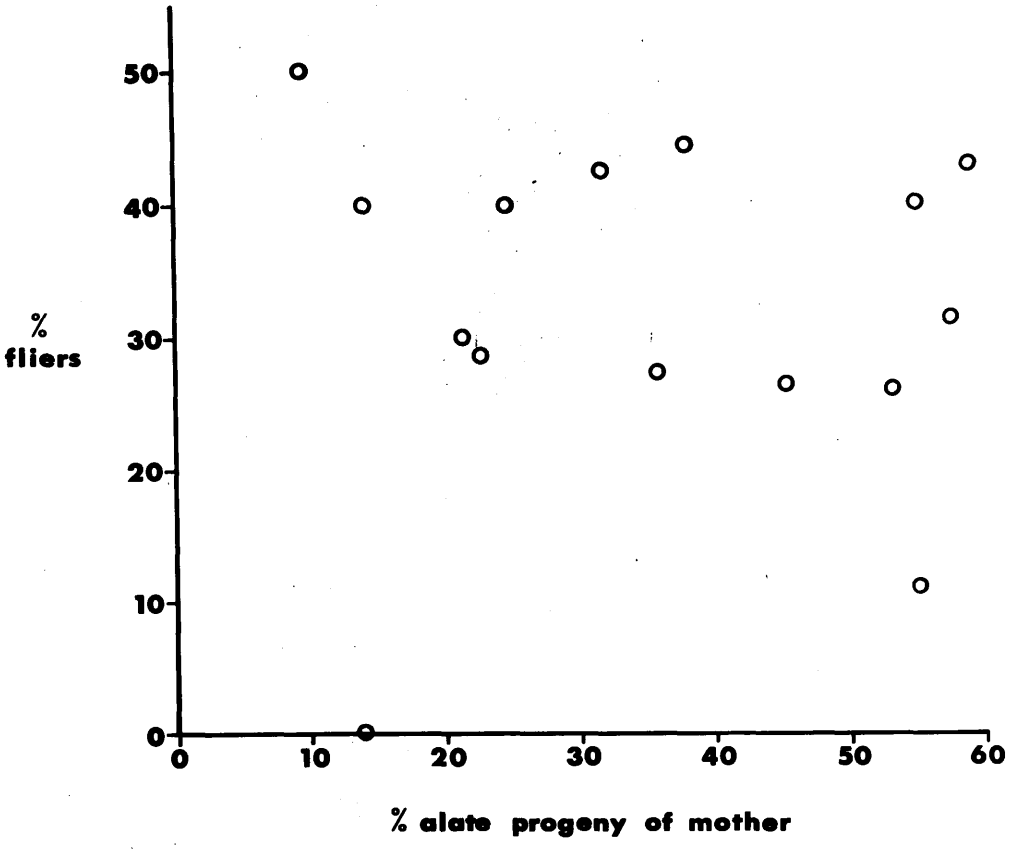

50
40
30
20
10
0
% fliers
0
10
20
30
40
50
60
% alate progeny of mother

Figure 4. Percentage fliers arising when alatae are reared in crowds until the fourth instar and then isolated against percentage alate progeny of the mother.

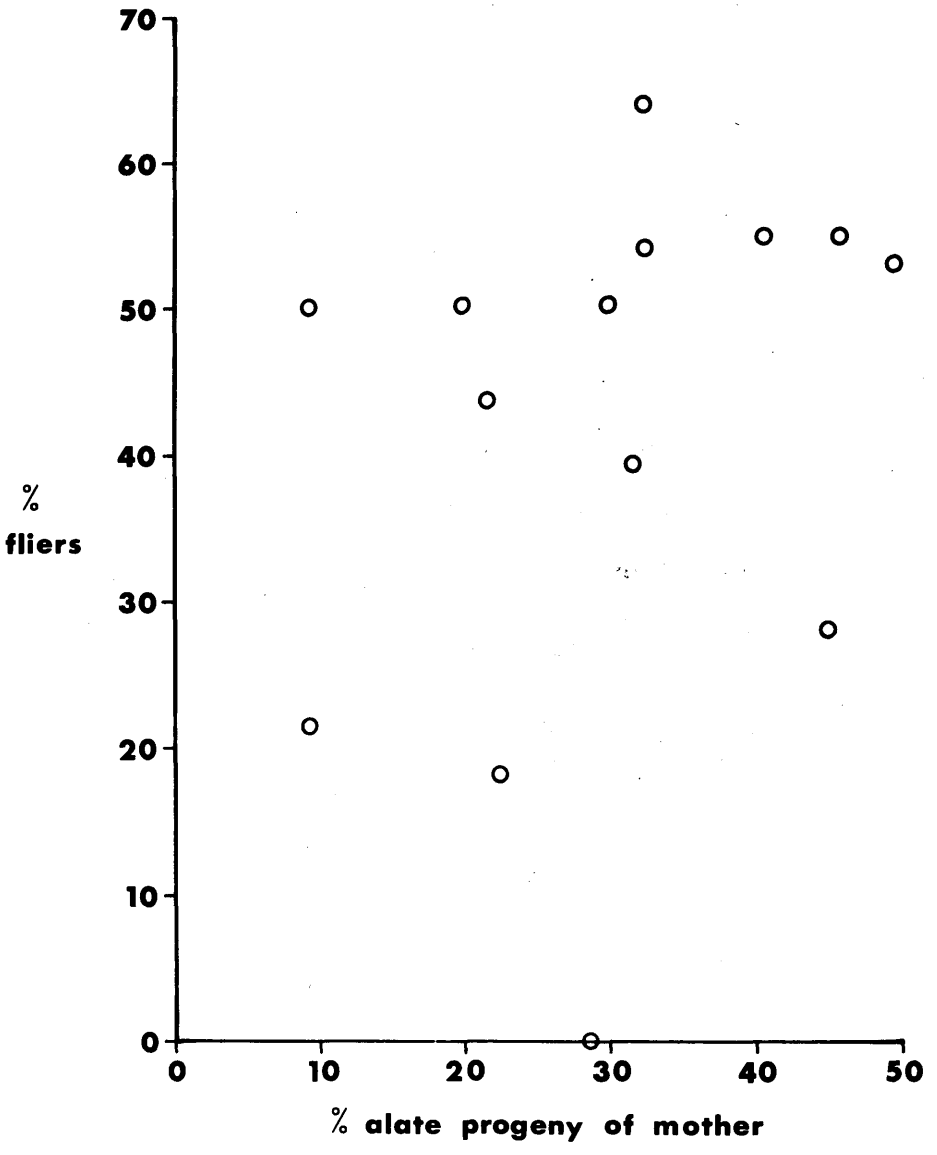
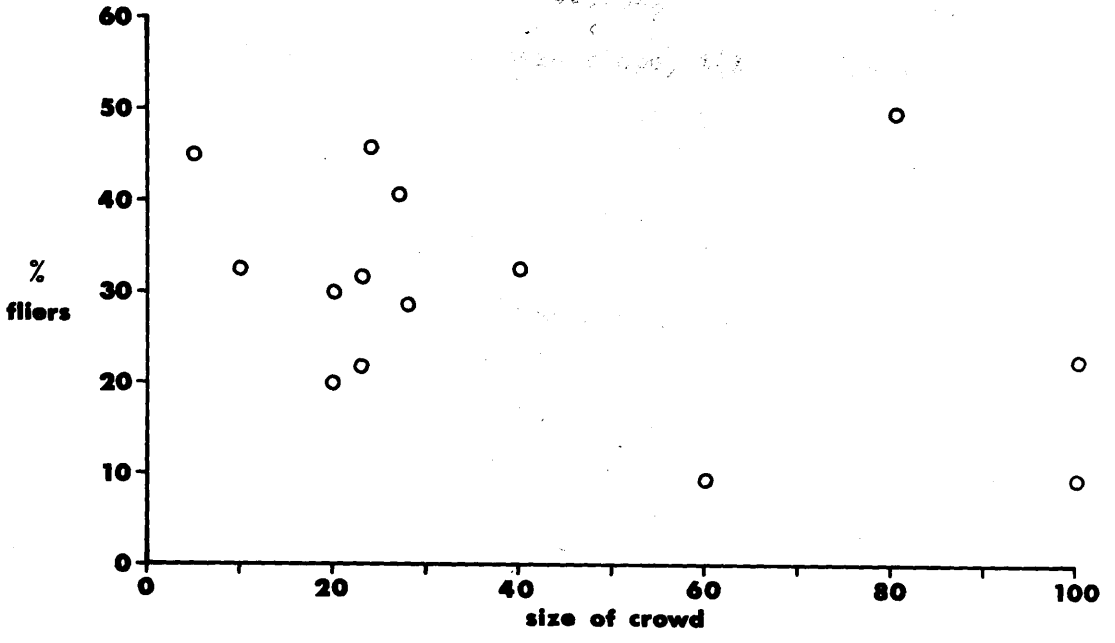

70
60
50
40
30
20
10
0
%
fliers
0
10
20
30
40
50
% alate progeny of mother

Figure 5. Percentage fliers arising when alatae are crowded until the fourth instar and then isolated against the size of crowd in which they were reared.


60
50
40
30
20
10
0
%
fliers
0
20
40
60
80
100
size of crowd

(1) $Y = 33.640 - 0.045X_1$ (i)

for comparison with zero slope, t = 0.2163,

d.f. = 13, not significant.

(2) $Y = 5.498 + 0.107X_1 + 0.383X_2$ (ii)

for comparison with zero slope, $t(X_1) = 0.351$,

d.f. = 5, not significant; $t(X_2) = 2.373$,

d.f. = 5, $P < 0.10$.

(3) $Y = 4.328 + 0.355X_1 + 0.505X_2$ (iii)

for comparison with zero slope, $t(X_1) = 1.659$,

d.f. = 15, not significant; $t(X_2) = 2.971$,

d.f. = 15, $P < 0.01$.

(4) $Y = 29.686 + 0.392X_1$ (iv)

for comparison with zero slope, t = 0,991,

d.f. = 12, not significant.

(5) $Y = 44.213 + 0.071X_2$ (iv)

for comparison with zero slope, t = 0.444,

d.f. = 12, not significant.

The situation where alatae were crowded to fourth instar and then isolated (iv) is described by equations 4 and 5 above. Analysis of the three factors involved, percentage fliers (Y), size of crowd ($X_2$) and the percentage alate progeny of the mother ($X_1$), by means of a multiple regression calculation similar to that used for ii and iii indicated that there was no significant correlation between Y and $X_1$ and Y and $X_2$. Each variable (X) was

Figure 6. The relationship between percentage fliers and percentage alate progeny of the mother and the size of crowd when alatae are crowded from first instar until the time of flight.

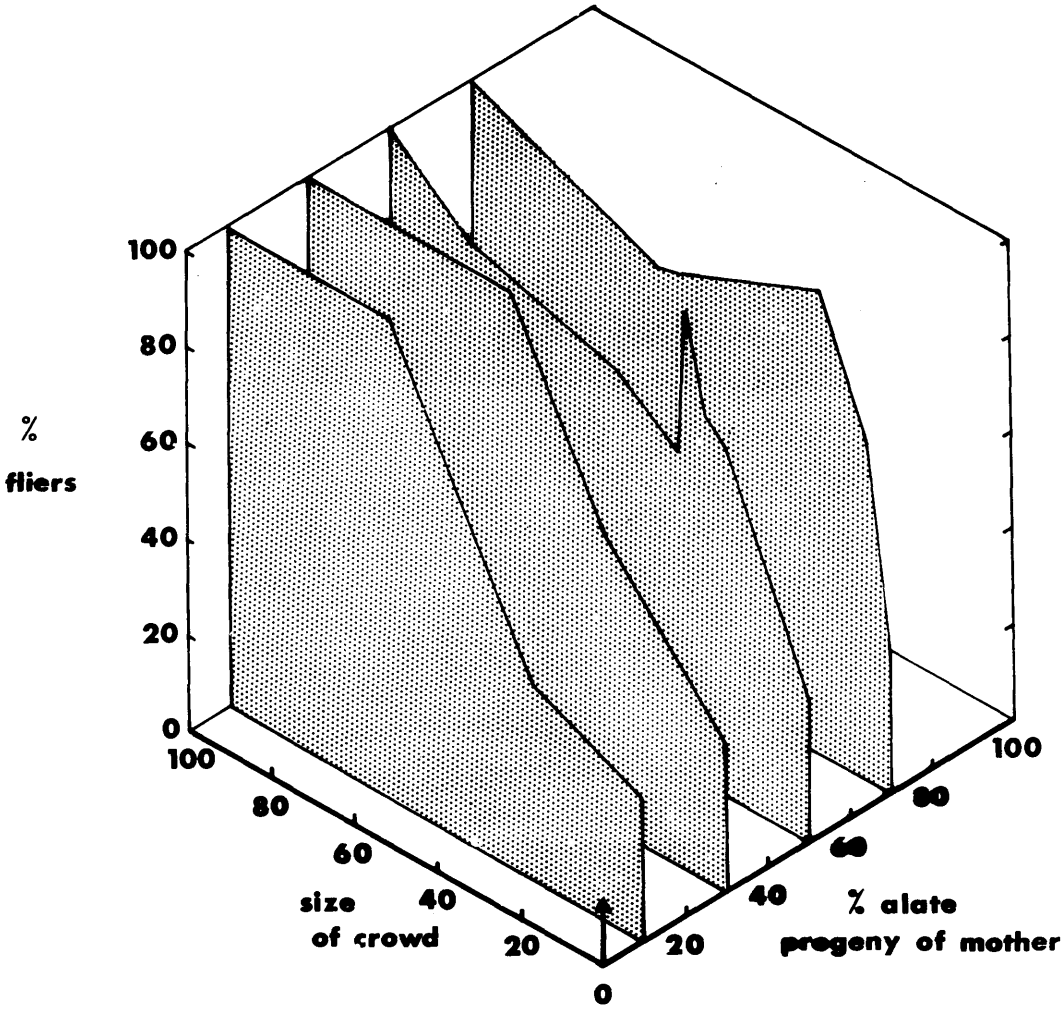
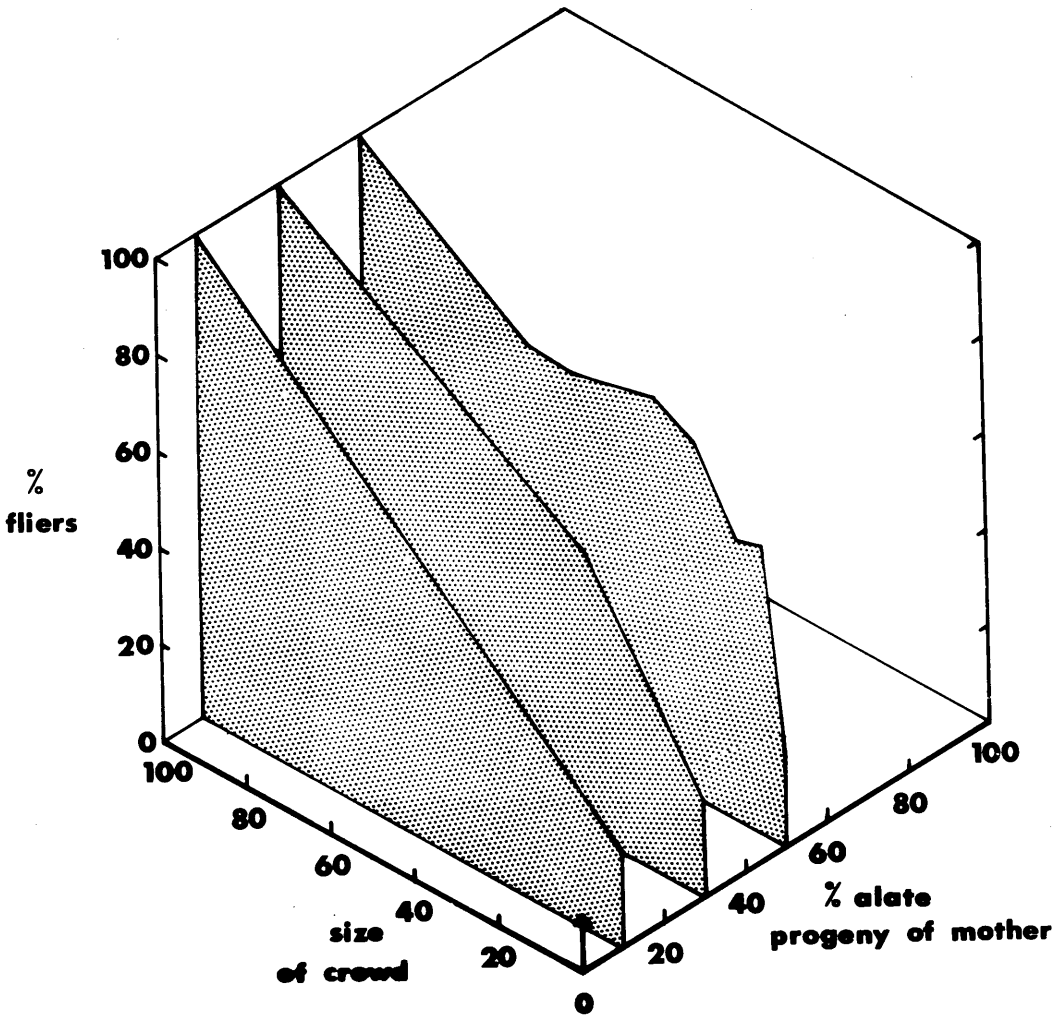

%
fliers
100
80
60
40
20
0
100
80
60
40
20
0
size
of crowd
100
80
60
40
20
0
% alate
progeny of mother

Figure 7. The relationship between percentage fliers and the percentage alate offspring of the mother and the size of crowd when alatae are isolated from first to fourth instar and then crowded.

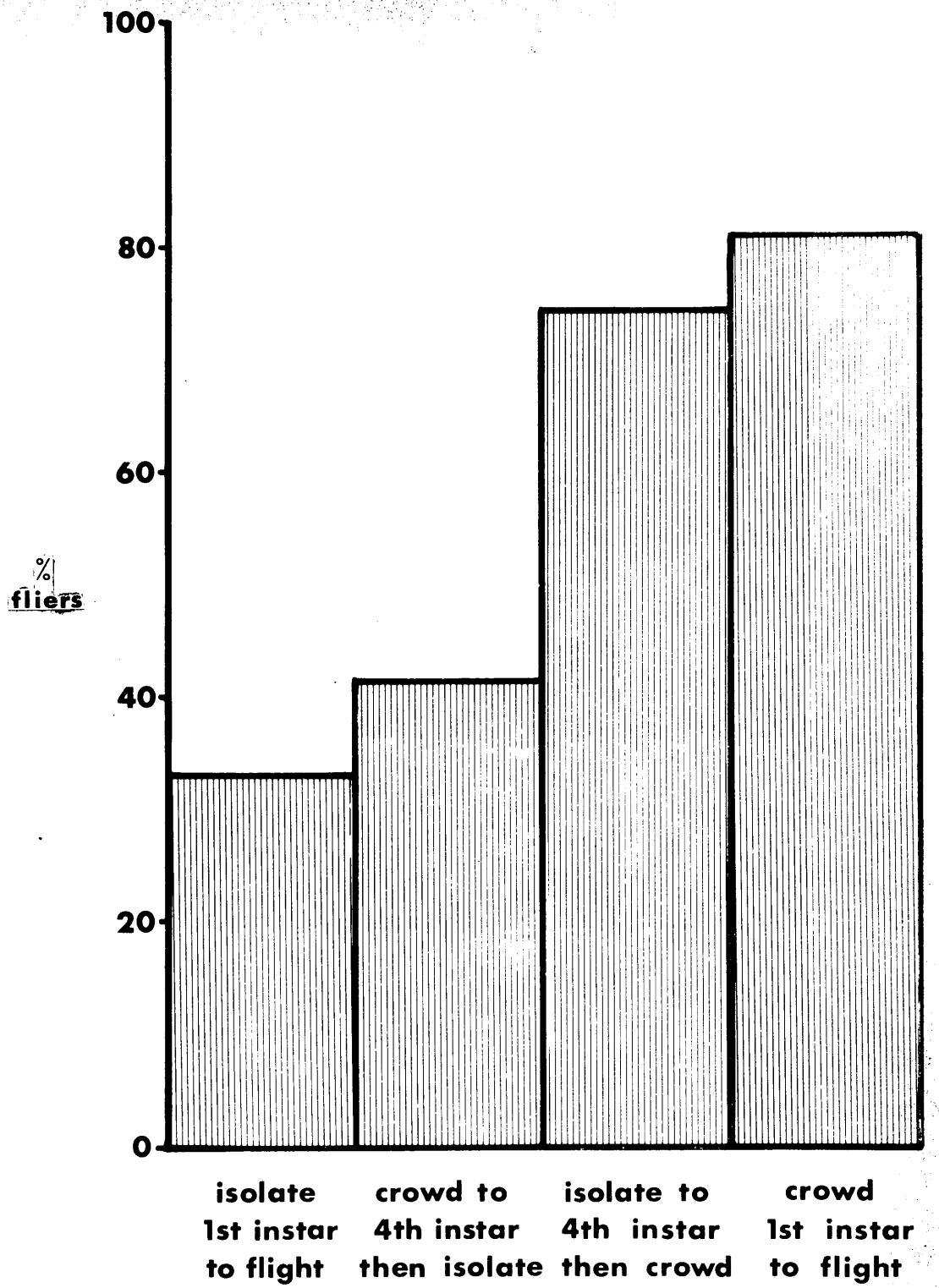

100
80
60
40
20
0
% fliers
100
80
60
40
20
0
size of crowd
100
80
60
40
20
0
% alate progeny of mother

recalculated using a simple regression analysis.

When alatae are isolated from fourth instar, no matter whether they have been in isolation or in crowds before this, a high proprtion of them remain on the plant. The mean percentage of aphids that fly is 32.1% ( 95% confidence limits 30.1% and 33.9% ) when alatae are isolated from day of birth and 41.4% ( 95% confidence limits 38.6% and 44.2% ) when they are isolated after the fourth instar ( Tables 1 and 2 in Appendix 1, Figures 3 and 4 ). When they are crowded at time of adult moult previous isolation does not significantly affect the numbers flying ( equation 2, Figure 6, Table 3 in Appendix 1 ), although fewer fly than when they have been crowded from birth ( equation 3, Figure 7, Table 4 in Appendix 1 ). In both cases where alatae were reared from birth in crowds the percentage of aphids flying is higher (iii and iv) than in situations where the alatae were isolated from birth (i and ii) ( Figure 8 ). Larval experience thus influences the number of alatae flying but this factor is outweighed by the effect of current conditions on their behaviour.

There is no significant relationship between percentage of alatae flying and the percentage alate progeny of the mother in any of the situations described above ( Figures 3, 4, 6 and 7 ). However, when alatae are crowded from birth to the adult moult the coefficient of the partial regression of percentage fliers (Y) on the percentage alate progenyof the mother ($X_1$ ) is

Figure 8. A simplified representation of the percentage of alatae flying when reared under different regimes of crowding and isolation.


100
80
60
%
fliers
40
20
0
isolate
1st instar
to flight
crowd to
4th instar
then isolate
isolate to
4th instar
then crowd
crowd
1st instar
to flight

significantly different from zero at the 20% level ( equation 3, Figure 7 ). This suggests that maternal experience may affect numbers flying in the following generation.

To determine whether there is any cumulative generation effect on flight one clone of apterae was reared in isolation for eight generations and a second reared in crowds of 30 for six generations. Both clones originated from the same apterous daughter of an alata. Each generation was monitored for response to crowding by taking adult apterae, siblings of those destined to be mothers of the next generation, crowding them ten at a time for 24 hours in a specimen tube, returning them to seedlings and subjecting the resulting offspring from day of birth to either isolation or crowding, 30 on one plant. The results are shown in Table 2.

Where alatae were isolated numbers are low. Large batches of larvae had to be isolated from each clone at the same time in order to obtain reasonable numbers of alatae and the bench space available limited the number of plants that could be used at one time.

Just after the alatae from generation 2 were put in the flight cabinet a fault in the temperature regulation system occurred and there was a sudden drastic fall in temperature from

Table 2. Numbers and percentages of alatae produced in successive generations by a clone of isolated and a clone of crowded apterae and the percentages of their alate offspring which fly as adults when subjected to different regimes of crowding and isolation.

| | | ISOLATED | | CROWDED | |
|---|---|---|---|---|---|
| Generation | %alatae | No. alatae | % fliers | No. alatae | % fliers |
| Isolated clone | | | | | |
| 1 | 12.3 | 0 | 0 | 9 | 55.6 |
| 2 | 3.2 | 1 | 100 | 0 | 0 |
| 3 | 14.6 | 2 | 0 | 5 | 100 |
| 4 | 42.9 | 5 | 29 | 13 | 61.5 |
| 5 | 39.1 | 9 | 37.5 | - | - |
| 6 | 29.4 | 10 | 10 | 15 | 53.3 |
| 8 | 15.6 | 5 | 40 | 9 | 100 |
| Crowded clone | | | | | |
| 1 | 27.6 | 4 | 50 | 12 | 75 |
| 3 | 30.5 | 4 | 25 | 21 | 85.7 |
| 4 | 29.2 | - | - | 7 | 71.4 |
| 6 | 29.2 | 3 | 0 | 16 | 93.8 |

20°C to 10°C within a few hours. The effect of this was to produce an increase in numbers, of both isolated and crowded alatae, taking off. Generation 2 of the crowded clone is therefore not included in Table 2.

In the crowded clone the percentage of alatae produced did not change appreciably over six generations. This was contrary to the results obtained with the isolated clone which fluctuated wildly from generation to generation ( Table 2 ).

There is no cumulative effect of isolation or crowding of the mothers on the percentage of offspring flying when alatae are crowded or isolated from birth. The length of time ( 3 months ) taken for this experiment and the fact that all available space had to be used prevented a repeat of the work.

## 3(b). ACTIVITY OF APTERAE

Observations of the activity of apterae on plants showed that when they were crowded they became more restless and left the plant more readily. On single plants with single growing points there is a negative correlation between the size of crowd on the plant and the length of time an adult aptera from that colony will remain on the plant ( Table 3 ). Apterae were marked with spots of non-toxic enamel paint on the dorsal surface of the abdomen. In colonies of 60 aphids and more the tendency was for previously isolated apterae to move around the middle of the plant and downwards but in smaller crowds the apterae moved up towards the growing point and stayed there ( Table 3 ). Newly moulted apterae in a large colony consisting of third and fourth instars were seen to wander about on the plant. Within two days all the fourth instar larvae had moulted to adult and all but three had left the plant. Apterae reared in crowds settled down when isolated on seedlings but wandered off the plant within a few days when placed on heavily infested plants.

Apterae placed singly on plants with more than one growing point moved up and down the shoots remaining for a few days at each growing point where they deposited larvae. The plants were covered systematically by movements up the shoots to the tips followed by downward movements until a shoot or leaf which was growing upward was encountered. In this way most of the plant was covered

Table 3. Movement of individual marked apterae on plants supporting M. viciae colonies of different sizes.

| Size of colony | 200 | 100 | 80 | 60 | 30 | 20 | 10 | 10 | 8 | 6 |
|---|---|---|---|---|---|---|---|---|---|---|
| No. of adults | 8 | 6 | 5 | 2 | 2 | 1 | 1 | 1 | 1 | 1 |
| Day aptera left plant | 4 | 6 | 4 | 5 | - | - | - | - | - | - |
| Movement of aptera | Around middle | Middle→top→middle | At top moving down | Middle | Top of side shoot | →top, stayed | Gradually moved up from middle | →top, stayed | →top, stayed | main stem & up |

before, on one last downward excursion, the aphid left the plant.

Apterae and alatae behave similarly in isolated and crowded conditions. Isolation promotes settling, feeding and reproduction while crowding causes movement over the plant and eventual migration either by flight or by walking.

## 3(c). BEHAVIOUR OF INDIVIDUAL ALATAE BEFORE FLIGHT

One day after adult moult fliers become very active and wander over the plant ( Figure 9a ) until they find a high and unobstructed point on the plant from which to take off.

It is probable that they do not feed between adult moult and flight, since an alata which is about to fly weighs considerably less than one which has just moulted. The difference appears to be due to water loss as shown by the regression of dry weight (Y) on live weight (X) for newly moulted immediately preflight alatae ( Figure 10 ). The equations for the regression are;

$$Y = 0.338X - 0.173 \qquad (1)$$

for newly moulted alatae and

$$Y = 0.356X - 0.074 \qquad (2)$$

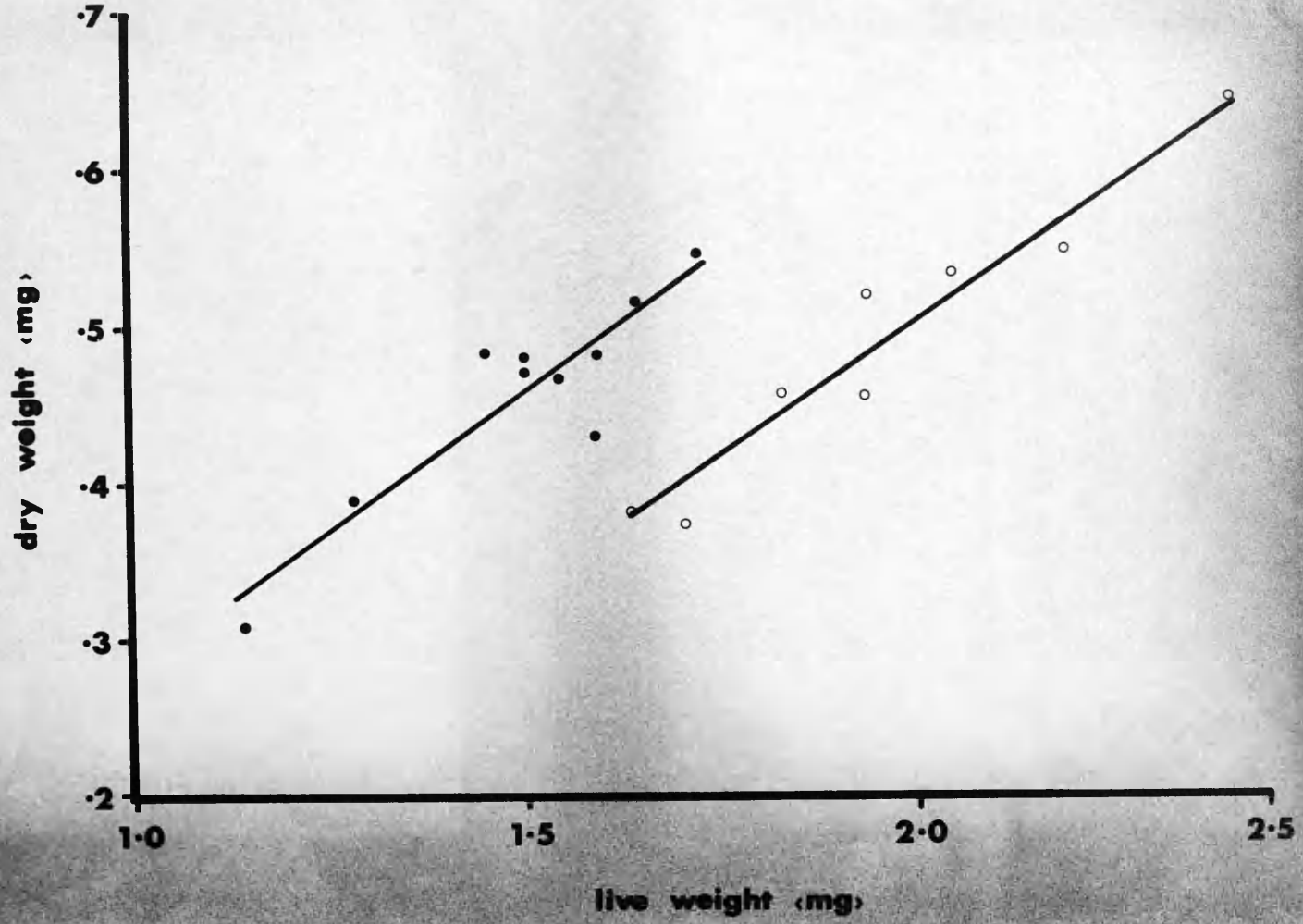
for preflight alatae.

All the alatae were taken from the same population on the same day. Over the whole range of weights the alatae lose the same quantity of water so that small alatae suffer a much greater water loss relative to weight ( comparison of slopes of equations 1 and 2, $t = 0.0532$, d.f. = 14, not significant ). An alata weighing 1.5 mg at birth loses 33% of its live weight whereas

Figure 9 a. Alatae of M. viciae about to fly.

b. Alata of M. viciae which has begun to reproduce without flight with an aptera and larvae.

Figure 10. Regression of dry weight ( mg ) on live weight ( mg ) for alatae reared in crowds which have just moulted ( o ) and which are about to fly ( • ).


·7
·6
·5
·4
·3
·2
dry weight (mg)
1·0
1·5
2·0
2·5
live weight (mg)

## 3(d). SIZE OF CORPUS ALLATUM IN TENERAL FLIERS AND NON-FLIERS

The size of the corpus allatum of apterous individuals of B. brassicae was found to be twice as large as that of alatae at imaginal moult ( White, 1965 ).

Measurement of the corpora allata, by a stereologic technique (Freere & Wiebel, 1967 ), of crowded and isolated teneral alatae, i.e. potential fliers and non-fliers, indicated no difference in size of the corpus allatum of the two types of alatae ( Table 4 ). Differences between fliers and non-fliers are thus not expressed in terms of corpus allatum volume in the teneral animal.

Table 4. Mean relative size in stereologic units ( m ) and standard deviation of the mean ( s ) of corpora allata of isolated teneral and crowded teneral alatae of M. viciae. The two batches of data (size N) are compared using an F-test of variance.

| | m | N | s |
|---|---|---|---|
| Isolated teneral alatae | 32.1 | 42 | 6.1 |
| Crowded teneral alatae | 29.8 | 50 | 6.0 |

F = 1.042 ( d.f. = 41/49 ) not significant

## 3(e). LIGHT AND ELECTRON MICROSCOPE STUDIES OF FLIGHT MUSCLE

The condition of the dorso-ventral indirect flight muscles of flying and non-flying alatae was studied using both light and electon microscopes.

Light microscopy.

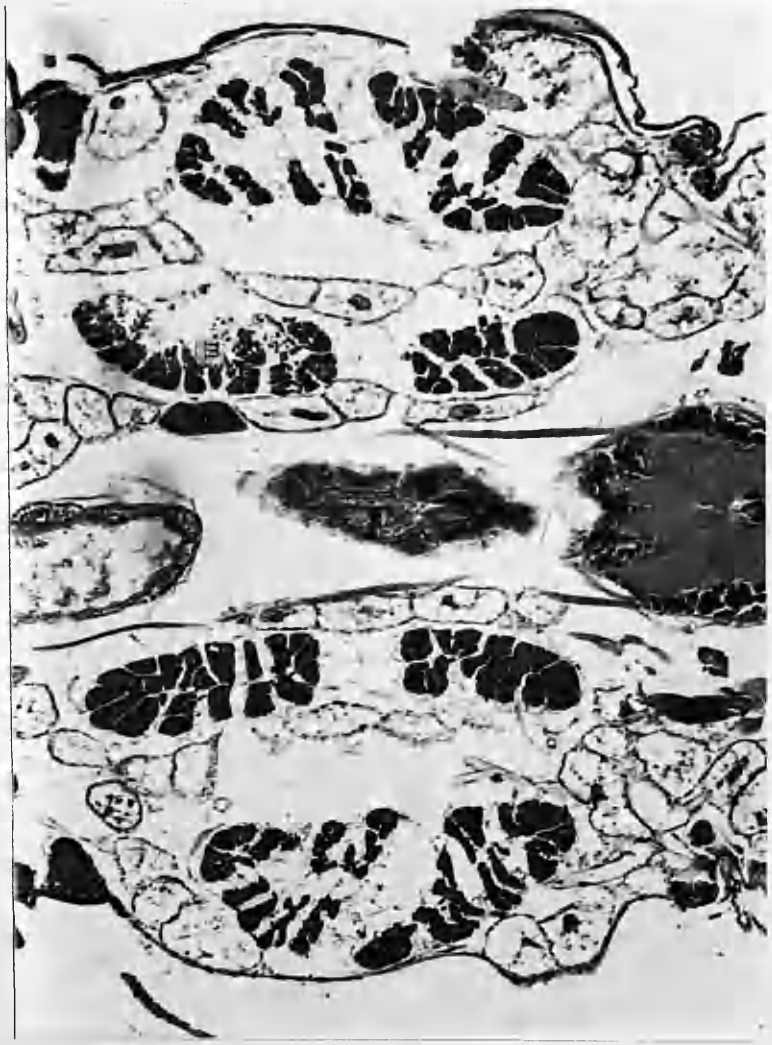
During the teneral period alatae reared in crowds and in isolation appear, under the light microscope to have identically intact wing muscles ( Figures 11a- 14a ). Flown alatae which have settled for 24 hours show a decrease in the thickness of the muscles viewed in transverse section. By the end of the second day after settling this is very marked ( Figures 11a, b ). Seven days after settling the indirect flight muscle has disappeared completely.

In non-flying alatae, degeneration of the indirect flight muscles appears to proceed at the same rate. As flight usually occurs about 24 hours after adult moult, 72 hours after the adult moult of non-fliers ( Figure 12b ) is taken to be equivalent to 48 hours after settling in fliers ( Figure 11b ).

In alatae that fly the breakdown of flight muscle starts within the first day after settling. This differs somewhat from previous findings where in M. viciae Kalt there was no histological

Figure 11. a. Transverse section through the dorso-ventral indirect flight muscles of a teneral crowded alata of *M. viciae*.
( *m* = muscle ) ( x 180 )

b. Transverse section through the dorso-ventral indirect flight muscles of a flier 2 days after settling. ( x 180 )



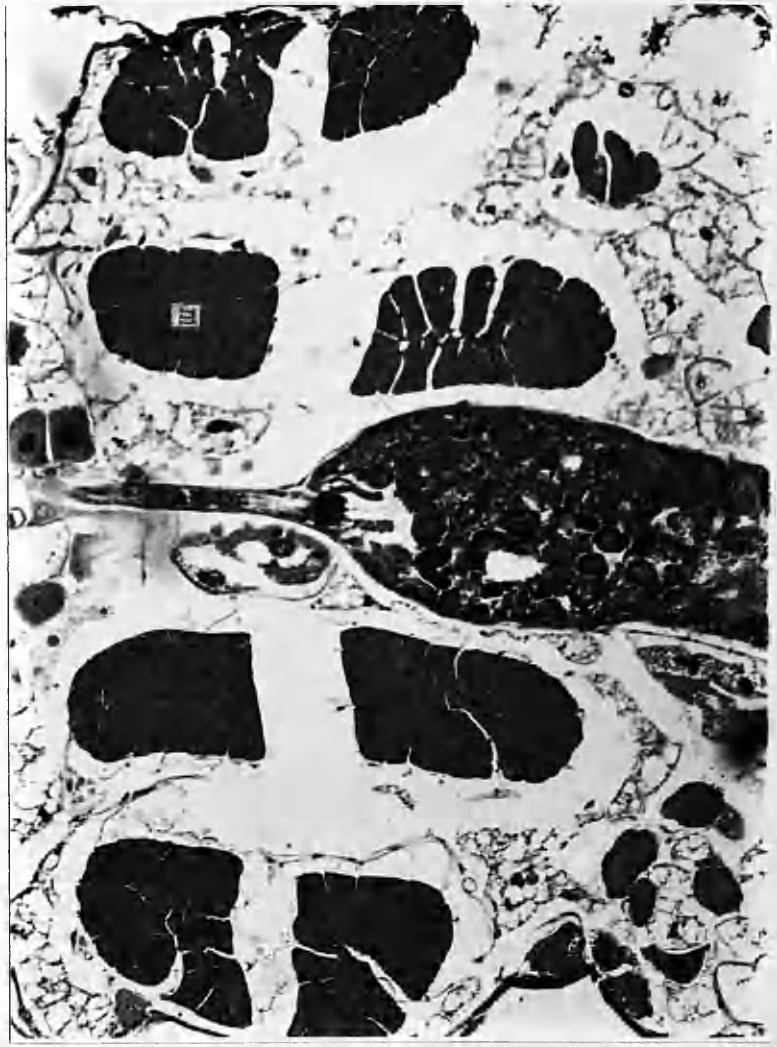
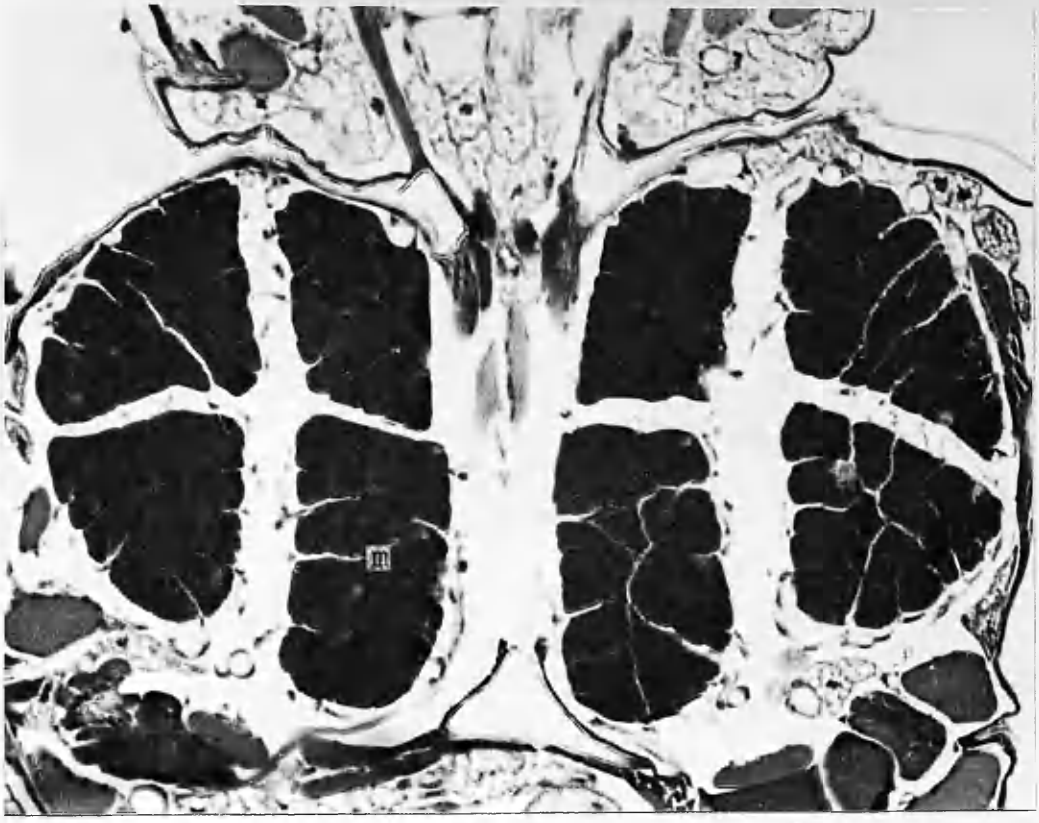


Figure 12. a. Transverse section through the dorso-ventral indirect flight muscles of a teneral isolated alata of M. viciae.
( m = muscle ). ( x 180 )

b. Transverse section through the dorso-ventral indirect flight muscles of a non-flier 2 days after settling. ( x 180)


m

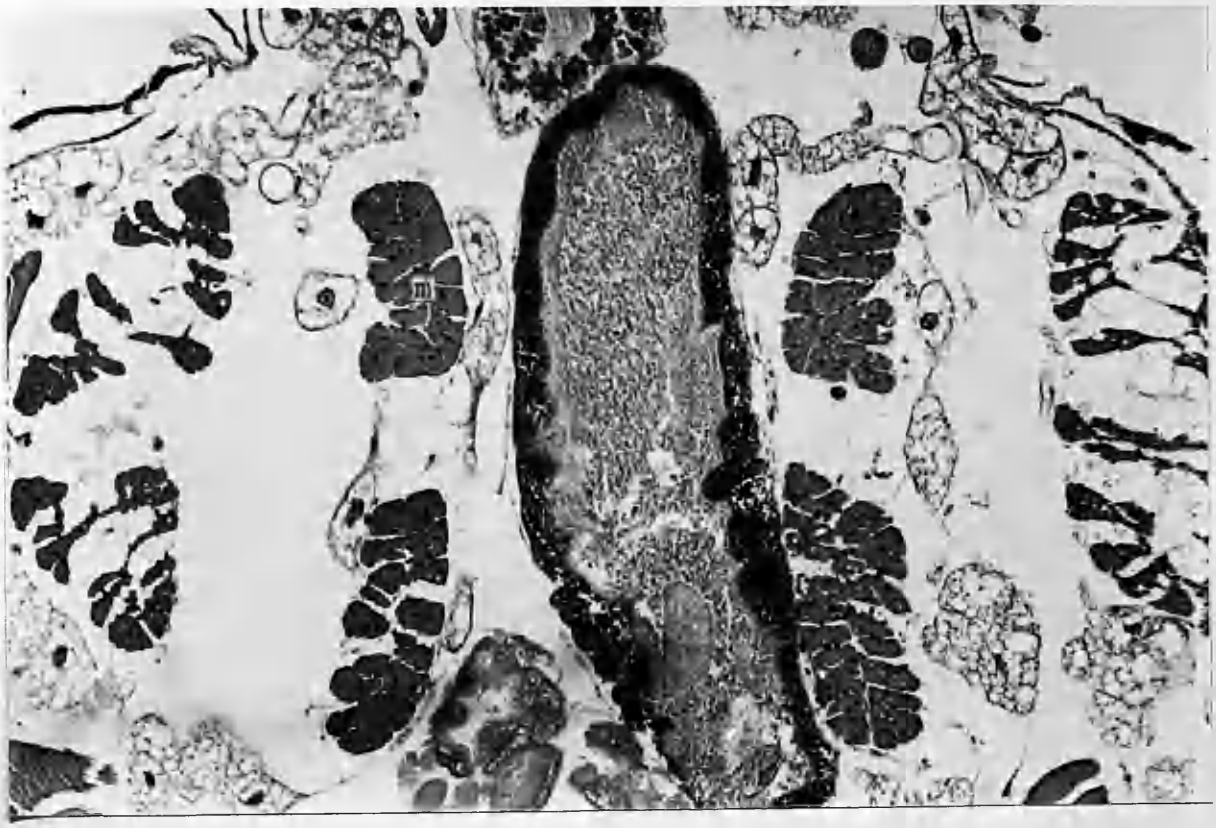
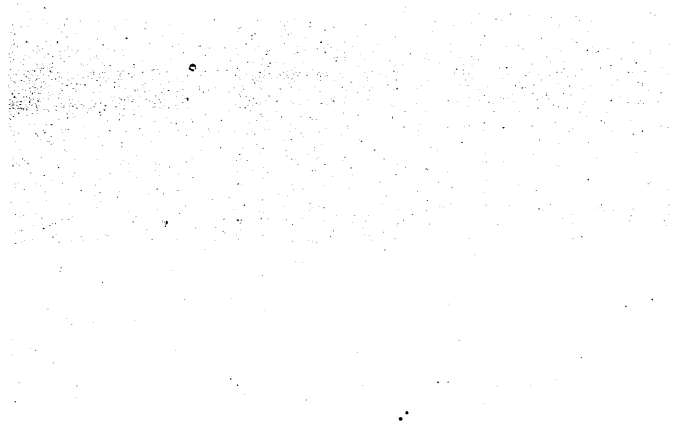
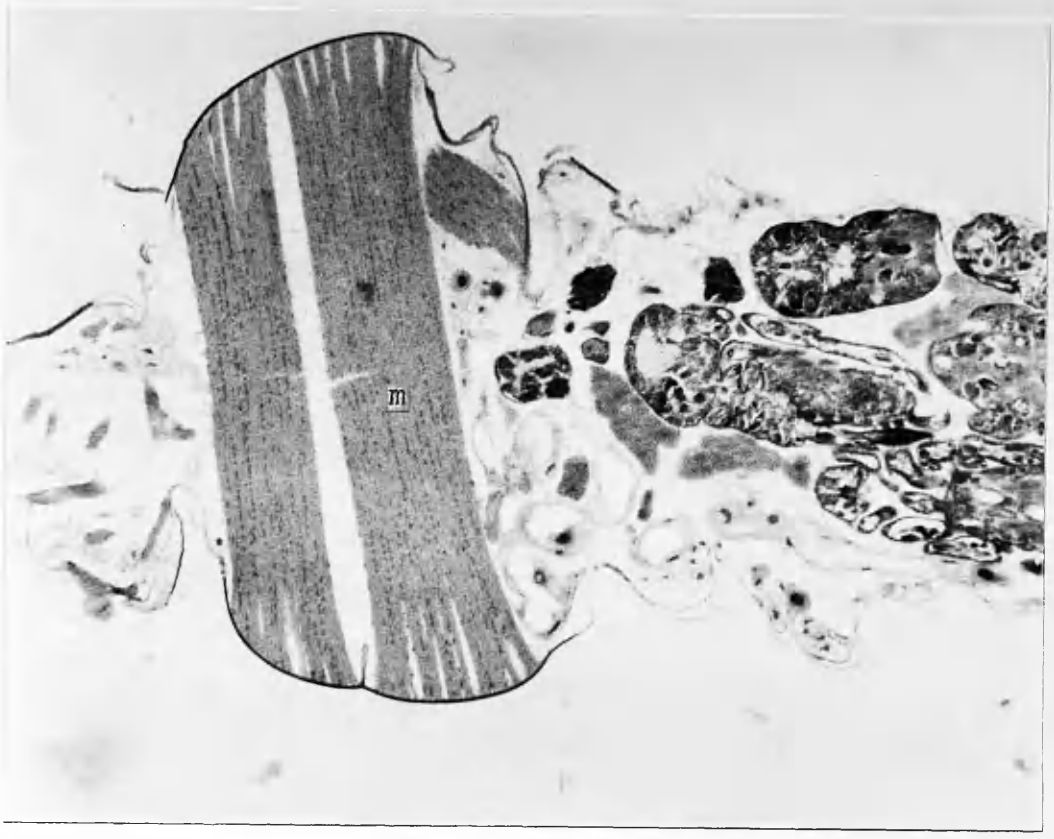

m

Figure 13. a. Longitudinal section through a crowded teneral alata of M. viciae showing a longitudinal section of the dorso-ventral indirect flight muscle ( m ).

( x 110 )



b. Longitudinal section through a flier 2 days after settling showing degeneration in the dorso-ventral indirect flight muscles ( m ). ( x 110 )


m

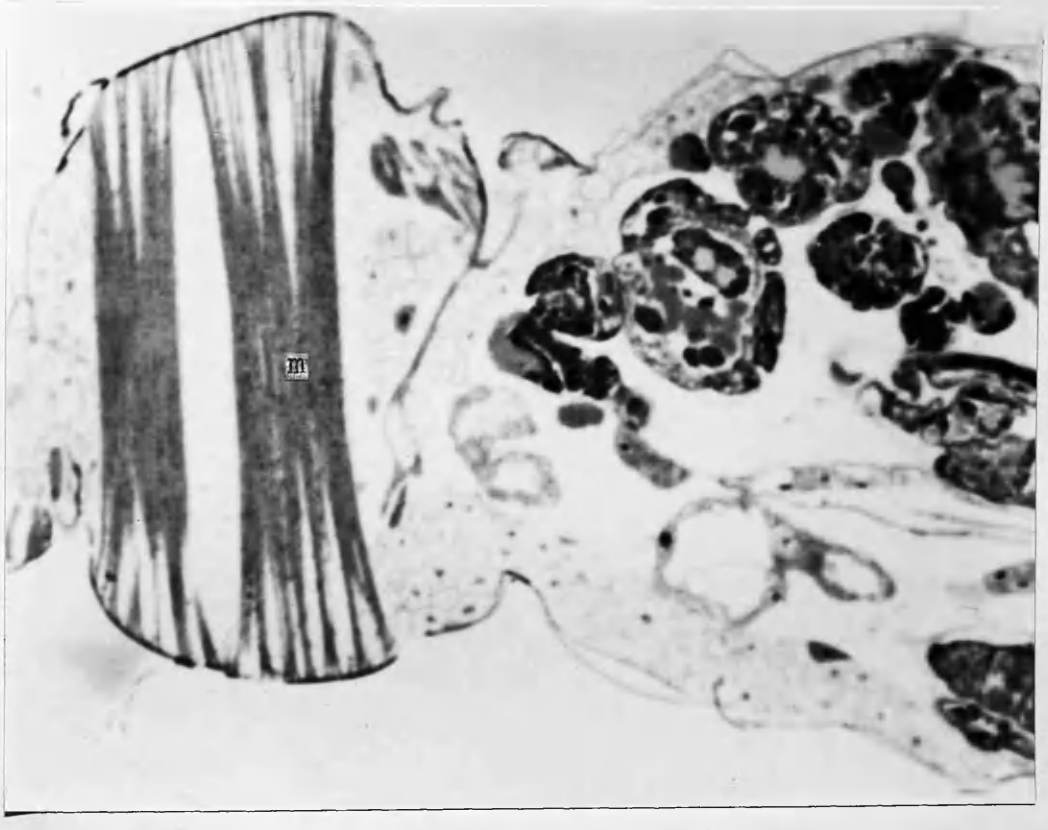
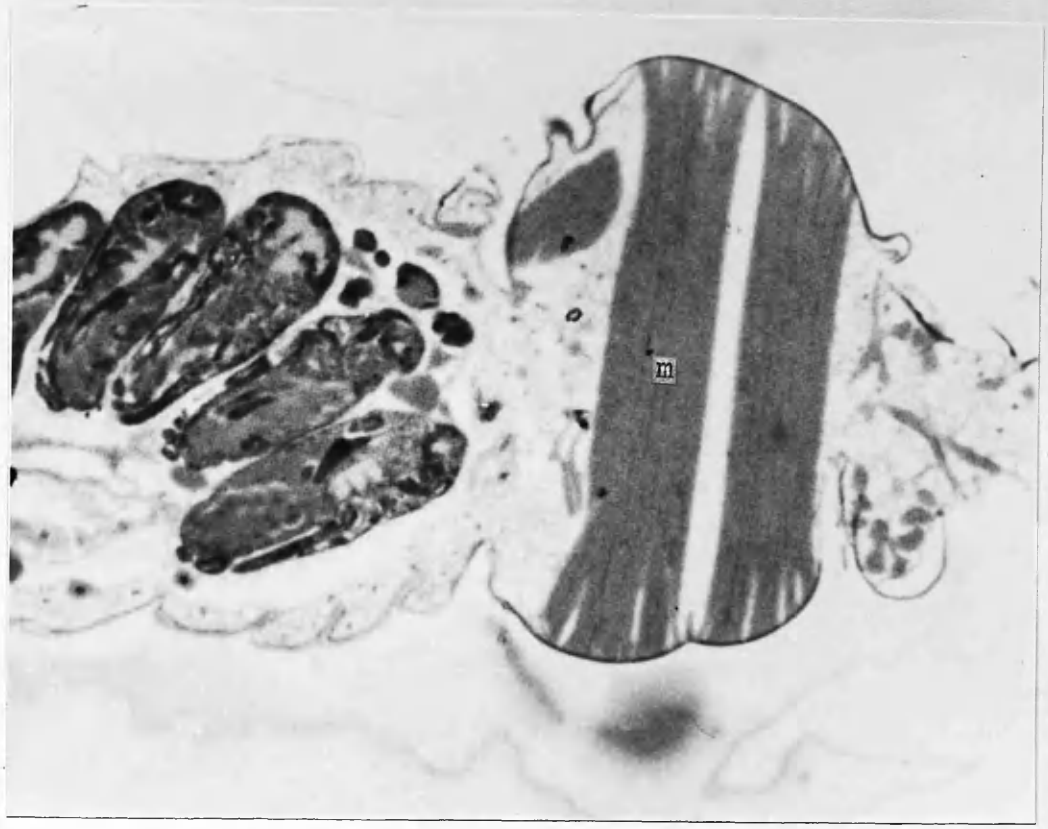

m

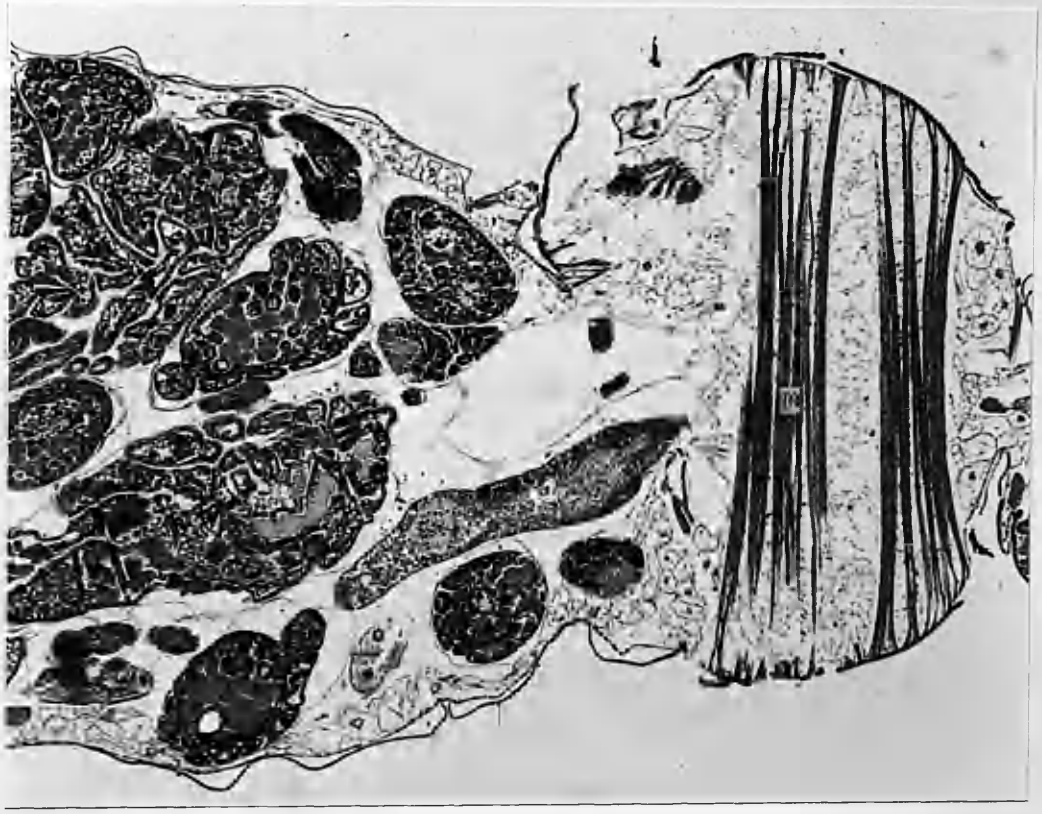
Figure 14. a. Longitudinal section through a teneral isolated alata of M. viciae showing the dorso-ventral indirect flight muscles ( m ) in longitudinal section.

( x 110 )

b. Longitudinal section through an isolated alata of M. viciae 3 days after moult. The muscle ( m ) shows signs of degeneration.

( x 110 )


m


m

evidence of breakdown until the third day after settling ( Johnson, 1957 ). The indirect flight muscle in M. viciae alatae reared in isolation appears to be intact until at least 12 hours after the adult moult ( Figure 2a ). In 42 of these teneral isolated alatae no evidence of muscle breakdown was found.

Electron microscopy.

A more detailed examination of the dorso-ventral indirect flight muscles was carried out using an electron microscope.

The ratio of mitochondrial area to muscle area and also the mean cross-sectional area of the muscle fibrils in $\mu^2$ for each specimen were calculated.

The differences expected in the results were changes in the size of the muscle fibrils (m) due to erosion of myosin from the edges (e) ( Figure 15b ), changes in the numbers of mitochondria (s) ( Figure15a ) and in their size. Changes of this nature are reported when the retractor unguis muscle of the locust is denervated ( Rees, 1971 ). The time scale in the locust is much greater ( after 70 days 20% of the muscle still remains ) than in the indirect flight muscle of M. viciae ( after 7 days all the muscle has gone ). First signs of degeneration in the locust are in the nerve endings ( Rees, 1971 ). Only two nerve endings

were found in the M. viciae preparations and so changes in the muscle only are considered here.

The abdominal intersegmental muscles of the moth, Antheraea pernyi, degenerate within 48 hours of the adult moult ( Lockshin & Williams, 1965a ). As early as the 5th hour after adult moult the first traces of degeneration are seen as scattered areas of erosion of the myofibrils and a slight contraction of the mitochondria. After 15 hours the muscle is reduced in volume to about one third, the myofibrils are disorganised and many of the myofilaments presumably destroyed by lysosome-like bodies. The nuclei have become pycnotic and the mitochondria are greatly shrunken and degenerate. During the degeneration process lipid deposits are observed near the mitochondria. Breakdown of the abdominal intersegmental muscles in A. pernyi has been shown to be a hormonal process primed during pupal life and triggered off by a sudden halt or decrease in the motor nerve activity to the intersegmental muscles. The muscles are capable of responding to this change in nervous information during the three days prior to ecdysis ( Lockshin & Williams, 1964, 1965b).

The breakdown of the wing muscles in M. viciae appears to be more similar to that in A. pernyi than to the degeneration due to denervation in locust.

Figure 15. a. Transverse section of the dorso-ventral indirect flight muscle of a flier 24 hours after moult showing muscle fibrils ( m ) and mitochondria ( s ). ( x 12,000 )

b. Transverse section of the dorso-ventral indirect flight muscle of a flier 48 hours after settling showing degenerating muscle fibrils ( m ), degenerating mitochondria ( ds ), a few small intact mitochondria ( s ) and erosion of myosin from the outer edge of the muscle fibrils ( e ).
( x 12,000 )


s
m

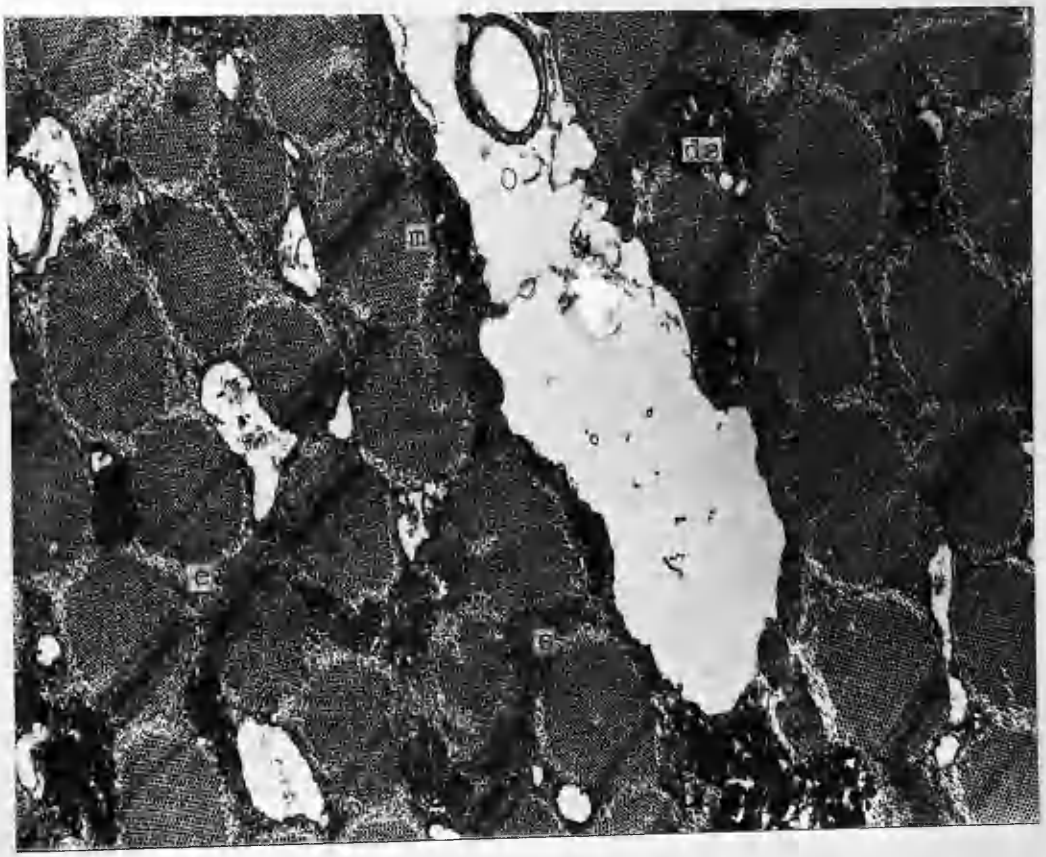
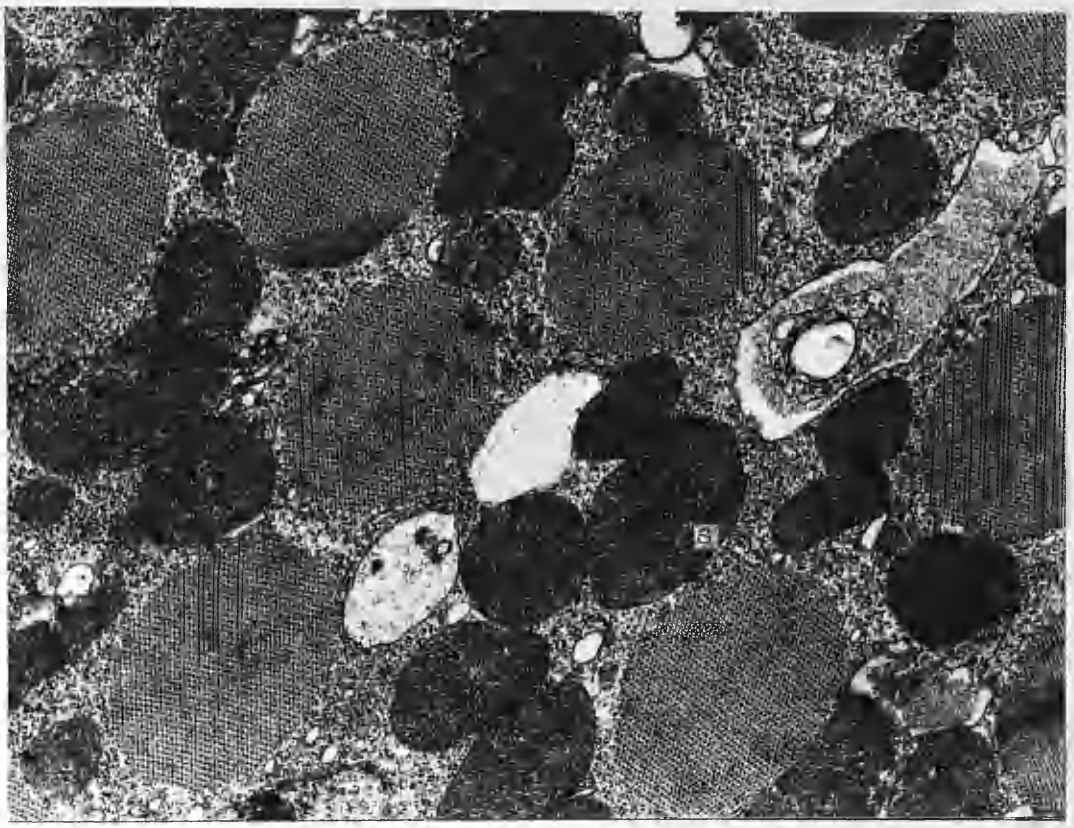

de
m
e
e

Figure 16. a. Transverse section of the dorso-ventral indirect flight muscle of a non-flier 24 hours after moult. The muscle fibrils ( m ) are intact but the mitochondria ( s ) are not as tightly packed together as in the muscle of a flier of the same age ( Figure 5a ).

( x 12,000 )

b. Transverse section through the dorso-ventral indirect flight muscle of a non-flier 72 hours after moult showing degenerated muscle fibrils ( m ), degenerating mitochondria ( ds ) and a few intact mitochondria ( s ). ( x 12,000 )


S


S
ds
M

Table 5. Mitochondria/muscle area ratios (mito/musc) and muscle fibril cross-sectional areas ($\mu^2$) for fliers and non-fliers at different times after adult moult.

| | FLIERS | | NON-FLIERS | |
|---|---|---|---|---|
| | Within 12 hours of moult. | | | |
| | mito/musc | musc $\mu^2$ | mito/musc | musc $\mu^2$ |
| | 0.70 | 2.56 | 1.15 | 2.94 |
| | 0.55 | 2.53 | 0.66 | 2.33 |
| | 1.01 | 2.99 | 0.91 | 2.24 |
| | 0.60 | 3.52 | | |
| | 0.90 | 1.70 | | |
| mean | 0.75 | 2.66 | 0.91 | 2.50 |
| | Within 24 hours of moult (i.e. time of flight for fliers). | | | |
| | mito/musc | musc $\mu^2$ | mito/musc | musc $\mu^2$ |
| | 0.89 | 4.12 | 0.64 | 3.23 |
| | 1.12 | 3.31 | 0.74 | 2.29 |
| | 1.07 | 3.32 | 0.75 | 3.28 |
| | 0.86 | 2.34 | 0.79 | 2.70 |
| | 0.89 | 2.18 | 0.64 | 1.90 |
| | 0.80 | 2.54 | | |
| | 1.14 | 2.42 | | |
| | 0.71 | 1.86 | | |
| | 1.12 | 1.62 | | |
| | 1.00 | 2.40 | | |
| mean | 0.97 | 2.61 | 0.71 | 2.68 |

Table 5 (continued).

| | FLIERS | | NON-FLIERS | |
|---|---|---|---|---|
| | 4 hours after settling. | | | |
| | mito/musc | musc $\mu^2$ | mito/musc | musc $\mu^2$ |
| | 0.53 | 5.02 | | |
| | 0.70 | 3.81 | | |
| | 0.61 | 1.64 | | |
| | 0.88 | 1.61 | | |
| | 0.70 | 1.88 | | |
| | 0.69 | 2.73 | | |
| | 1.03 | 3.35 | | |
| | 0.70 | 1.33 | | |
| | 0.61 | 2.34 | | |
| | 0.74 | 2.48 | | |
| mean | 0.72 | 2.62 | | |
| | One day after settling, 48 hours from moult. | | | |
| | mito/musc | musc $\mu^2$ | mito/musc | musc $\mu^2$ |
| | | | 0.90 | 2.33 |
| | | | 0.88 | 2.55 |
| | | | 0.96 | 2.68 |
| mean | | | 0.91 | 2.68 |
| | Two days after settling, 72 hours after moult. | | | |
| | mito/musc | musc $\mu^2$ | mito/musc | musc $\mu^2$ |
| | 0.25 | 0.95 | 0.03 | 0.63 |
| | 0.08 | 1.19 | 0.17 | 0.46 |
| | 0.05 | 1.40 | 0.11 | 0.85 |
| | 0.13 | 1.44 | | |
| mean | 0.13 | 1.25 | 0.10 | 0.65 |

As little as 4 hours after settling a significant decrease ( $P < 0.01$ ) is seen in the mitochondria/muscle area ratio of flown aphids ( Table 5 ) although no decrease in the size of the muscle bundles is apparent at this time. Two days after settling the muscle fibrils have decreased to 50% of their original cross-sectional area and the mitochondria are much reduced in number and size ( Table 5, Figures 15a,b ). Myosin is lost from the edges of the muscle bundles (e, Figure 15b ).

12 hours after adult moult the wing musculature of alatae reared in crowds and in isolation is the same in terms of mitochondria and muscle ( Table 5 ). Aphids reared in isolation, however, do not possess as great a number of mitochondria in their wing muscles 24 hours after moult as do their flying counterparts of the same age ( $P < 0.01$ ) ( Table 5, Figures 15a, 16a ).

Although the light microscope studies reveal a decrease in the muscle size in non-fliers 48 hours after moult the non-flying aphids used for electron microscopy showed no change in muscle fibril size from 12 hours to 48 hours after adult moult ( Table 5 ).

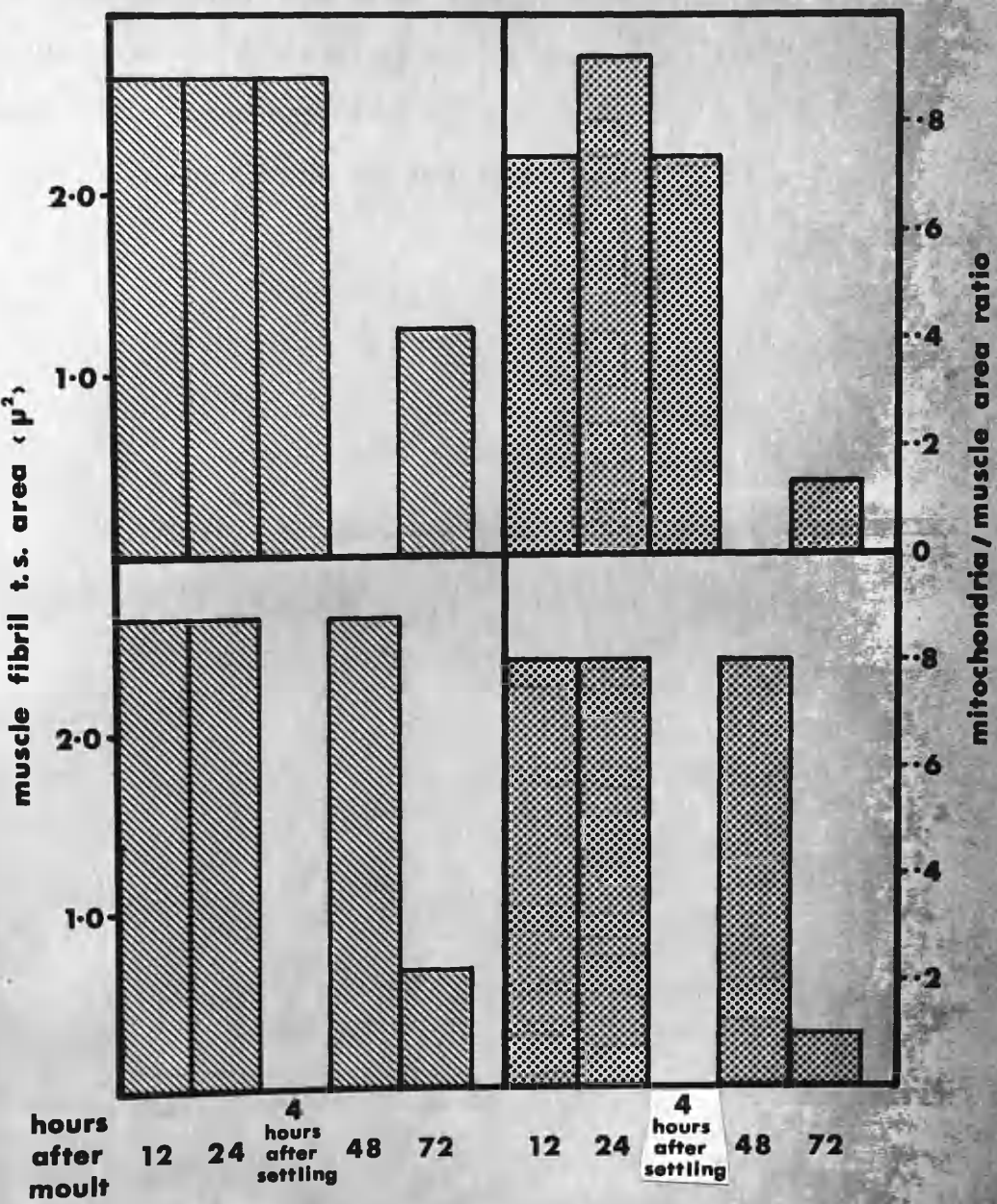
The more advanced state of breakdown of the muscle fibrils in non-fliers 72 hours after moult compared with fliers which have settled for 2 days suggests that the degeneration is initiated before the end of the first day after the adult moult ( Figures 15b,

16b ). In fliers the initiation of breakdown is delayed until after settling.

The time required to complete the loss of indirect flight muscle in M. viciae is longer ( about 7 days ) than the 2 days necessary for the disappearance of the abdominal intersegmental muscles of A. pernyi. However, within 72 hours of moult the muscle fibrils of fliers have been reduced to 50% of their original volume and those of non-fliers to 25% of their original volume ( Table 5, Figure 17 ). Most of this loss has taken place between 48 and 72 hours after moult so that the reduction of the flight muscles in M. viciae is very similar in terms of time to that of the abdominal intersegmental muscles of A. pernyi.

Although there is no evidence after 2 days of either the lipid deposits within the muscle or of the lysosome-like bodies reported in the perniid moth ( Lockshin & Williams, 1965a ) it is probable that degeneration is similarly controlled in both cases. In A. pernyi juvenile hormone is believed to prevent muscle breakdown until after the adult moult ( Lockshin & Williams, 1964 ). A similar protective system may operate during the teneral period in M. viciae so that after about 24 hours, unless flight occurred, muscle breakdown would begin. When motor impulses to the wing muscles cease, as would happen when flying aphids settle, or if the muscle never receives any information from the nervous system, as may be the case with aphids which do not fly, muscle degeneration

Figure 17. Histograms showing where significant changes occur in muscle fibril cross-sectional area and in mitochondrial/muscle area ratio during flight muscle breakdown in flying and non-flying alatae of *M. viciae*.


muscle fibril t.s. area (μ²)
2·0
1·0
2·0
1·0
·8
·6
·4
·2
0
·8
·6
·4
·2
mitochondria / muscle area ratio
hours after moult
12
24
4 hours after settling
48
72
12
24
4 hours after settling
48
72

would be initiated.

Although some alatae of M. viciae do not fly they all possess intact wing muscles at least up to 12 hours after the adult moult. The degeneration process starts at the end of the teneral period ( 24 hours ) in non-fliers and immediately after settling in fliers.

## 3(f). REPRODUCTIVE RATES AND WEIGHTS OF LARVAE

Since non-flying alatae of M. viciae are structurally identical to those which fly this species presents the ideal situation for an investigation of the effect of flight on reproductive capacity.

Newly moulted apterous, and newly moulted flown and unflown alatae of M. viciae were isolated on bean seedlings. Apterae, fliers and non-fliers were weighed on the first day of reproduction. The larvae produced each day by each mother were counted, the day's production of each mother weighed as one batch and the mean weight of larvae produced by each aphid each day calculated.

After 20 days 70% of the apterae, 42.2% of the fliers and 42.5% of the non-fliers were still alive. Thus flight does not affect the longevity of alatae but there was a much higher mortality rate among the alatae than among the apterae. This situation is different from that in A. fabae. Alatae of A. fabae reared singly in the laboratory live just as long as apterae ( Dixon & Wratten, 1971 ).

The numbers of larvae (Y) produced by apterae and non-fliers do not vary significantly with the weight of the mother (X) during any of the 5 day periods from days 1 to 20 of reproductive life

Figure 18. ~~Mean~~ numbers of larvae produced during days 1-5 ( a ), 6-10 ( b ), 11-15 ( c ) and 16-20 ( d ) plotted against maternal weight ( mg ) measured on the first day of reproduction.

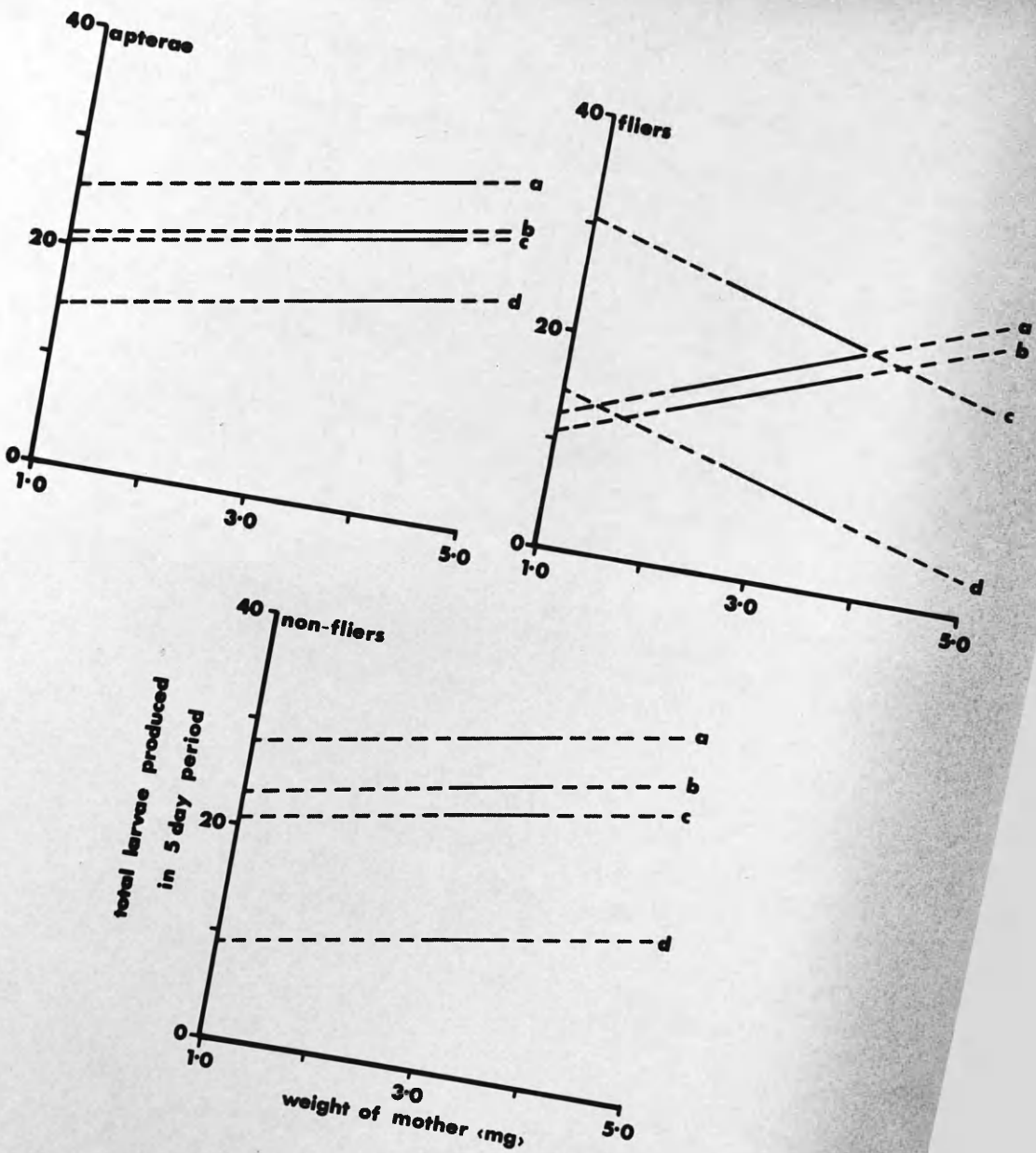

40
apterae
a
b
c
d
20
0
1·0
3·0
5·0
40
fliers
a
b
c
d
20
0
1·0
3·0
5·0
40
non-fliers
a
b
c
d
20
0
1·0
3·0
5·0
total larvae produced in 5 day period
weight of mother (mg)

Table 6. Regression formulae and the significance of the deviation from zero of the regression coefficients for the relationship between the number of aphids (Y) produced by apterae, fliers and non-fliers within days 1 - 5, 6 - 10, 11 - 15 and 16 - 20 of reproductive life and the weight of the mother in milligrams (X). The common regression coefficient is given for each group.

| 5 day period | No. of mothers | Regression formula | Sig. of deviation of regress. coeff. from zero | Common regr. coeff. |
|---|---|---|---|---|
| **Apterae** | | | | |
| 1 | 13 | $Y = 1.015X + 26.883$ | N. S. | 1.767 |
| 2 | 13 | $Y = 0.76X + 23.358$ | N. S. | |
| 3 | 13 | $Y = 1.068X + 21.285$ | N. S. | |
| 4 | 13 | $Y = 4.225X + 2.796$ | N. S. | |
| **Fliers** | | | | |
| 1 | 14 | $Y = 7.219X + 2.763$ | 0.01 | 6.119 |
| 2 | 14 | $Y = 5.251X + 6.993$ | 0.10 | |
| 3 | 9 | $Y = 40.309 - 5.225X$ | N. S. | -2.822 |
| 4 | 7 | $Y = 2.842X - 1.027$ | N. S. | |
| **Non-fliers** | | | | |
| 1 | 8 | $Y = 6.145X + 11.313$ | N. S. | -0.019 |
| 2 | 8 | $Y = 3.288X + 16.432$ | N. S. | |
| 3 | 6 | $Y = 36.342 - 3.342X$ | N. S. | |
| 4 | 5 | $Y = 0.107X + 13.152$ | N. S. | |

Table 7. Regression formulae for the relationship between the numbers of larvae (Y) produced by apterae, fliers and non-fliers during days 1 - 5, 6 - 10, 11 - 15 and 16 - 20 of reproductive life and the weight of the mother in milligrams (X) recalculated using the common regression coefficients from Table 6.

Apterae

| 5 day period | Regression formula using C.R.C. |
|---|---|
| 1 | $Y = 23.88 + 1.77X$ |
| 2 | $Y = 19.34 + 1.77X$ |
| 3 | $Y = 18.50 + 1.77X$ |
| 4 | $Y = 12.58 + 1.77X$ |

Fliers

| | |
|---|---|
| 1 | $Y = 6.55 + 6.12X$ |
| 2 | $Y = 4.48 + 6.12X$ |
| 3 | $Y = 33.47 - 2.82X$ |
| 4 | $Y = 17.54 - 2.82X$ |

Non-fliers

| | |
|---|---|
| 1 | $Y = 26.34 + 1.68X$ |
| 2 | $Y = 21.84 + 1.68X$ |
| 3 | $Y = 19.25 + 1.68X$ |
| 4 | $Y = 7.59 + 1.68X$ |

( Table 6, Figure 18 ). However, large alatae which fly produce significantly more larvae than small flown alatae during the first ten days of reproductive life ( days 1-5; $t = 3.786$, d.f. = 12, $P < 0.01$ and days 6-10; $t = 2.127$, d.f. = 12, $P < 0.10$ ) ( Table 6 ). There are differences in elevation of the regression lines ( Table 6 ) and this is made clearer by recalculating each line using the common regression coefficient. The resulting regressions for total number of larvae produced in a five day period (Y) against the weight of the mother (X) are shown in Table 7. From comparisons of the regression lines calculated using the common regression coefficient for apterae and non-fliers there appears to be no significant difference in the numbers produced by the two morphs during the four five day periods ( Table 1 in Appendix 2 ).

A very marked fall-off in larval production is seen in the last 5 day period for fliers when compared with apterae ( Figure 18, Table 1 in Appendix 2 ). During days 15 to 20 the numbers of larvae produced by apterae and non-fliers also falls off but not as drastically as for fliers ( Table 1 in Appendix 2 ). Non-fliers produce fewer larvae than apterae during days 15 to 20 and more than fliers during this time. The differences, however, are not significant ( Table 1 in Appendix 2 ). Apterae and non-fliers and those fliers which weigh more than 3.0 mg produce the greatest number of larvae during the first 5 day period. Small fliers produce the largest numbers during the third 5 day

period ( Figure 18 ).

Thus although longevity in alatae is not affected by flight, flying does seem to cost an alata a large proportion of its potential larva production. After flight larva production by small alatae is distributed differently in time. A larger proportion of larvae are produced by small fliers during days 6 to 15 of reproductive life than by large fliers, apterae and non-fliers over the same period.

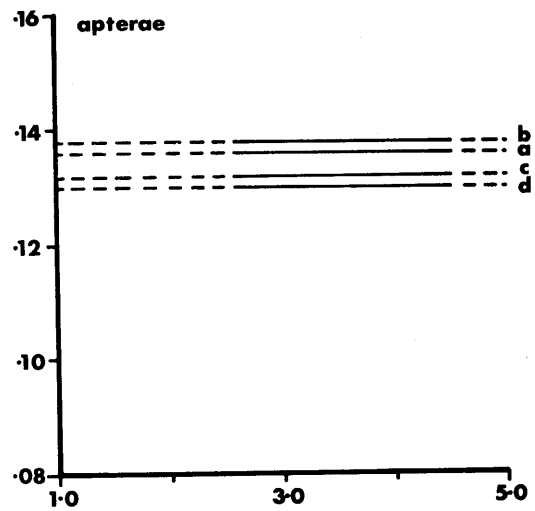
The regression equations for mean larval weight against maternal weight were recalculated using the common regression coefficient ( Table 11 ). The resulting equations are represented in Figure 19. After the first ten days the mean weight of larvae produced by apterae falls from 0.14 mg to 0.13 mg ( Figure 19, Table 2 in Appendix 2 ). Non-fliers produce the smallest larvae during the first 5 day period. Larger larvae are produced during days 6 to 10 and the largest during the second half of the reproductive period. In fliers also the smallest larvae are produced first. In A. fabae the weight of larvae produced by alatae increase with time while those produced by apterae remain the same ( Dixon & Wratten, 1971 ).

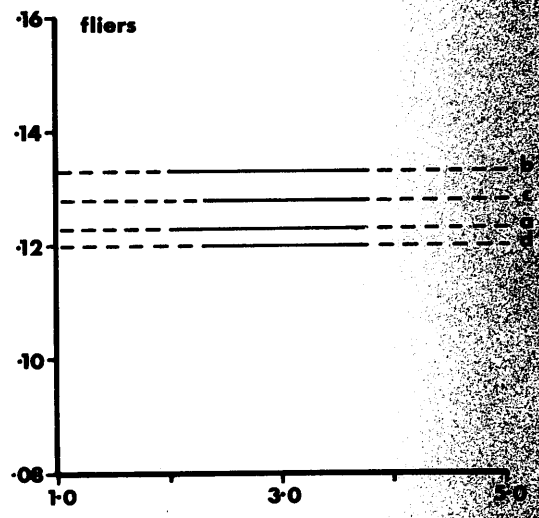
If larval production is calculated as the total mass of larval tissue produced by an aphid during days 1 to 5, 6 to 10,

Table 8. Total mass of larvae (mg) produced by 2.5 mg and 3.5 mg apterae, fliers and non-fliers during days 1 - 5, 6 - 10, 11 - 15 and 16 - 20 of reproductive life.

| Weight of mother (mg) | Total mass of larvae (mg) | | | | |
|---|---|---|---|---|---|
| | Days 1 - 5 | Days 6 - 10 | Days 11-15 | Days 16-20 | Total |
| APTERAE | | | | | |
| 2.5 | 4.485 | 3.198 | 3.133 | 1.585 | 12.401 |
| 3.5 | 4.298 | 3.513 | 3.279 | 2.235 | 13.325 |
| FLIERS | | | | | |
| 2.5 | 2.531 | 2.564 | 3.099 | 0.892 | 9.086 |
| 3.5 | 3.418 | 3.370 | 2.992 | 1.142 | 10.992 |
| NON-FLIERS | | | | | |
| 2.5 | 2.829 | 3.263 | 4.590 | 2.035 | 12.717 |
| 3.5 | 3.764 | 3.425 | 3.135 | 1.676 | 12.000 |

Figure 19. Mean larval weight ( mg ) during days 1-5 ( a ), 6-10 ( b ), 11-15 ( c ) and 16-20 ( d ) plotted against maternal weight ( mg ) measured on the first day of reproduction for apterae, fliers and non-fliers.


apterae
·16
·14
·12
·10
·08
1·0
3·0
5·0
b
a
c
d


fliers
·16
·14
·12
·10
·08
1·0
3·0
5·0
b
c
a
d

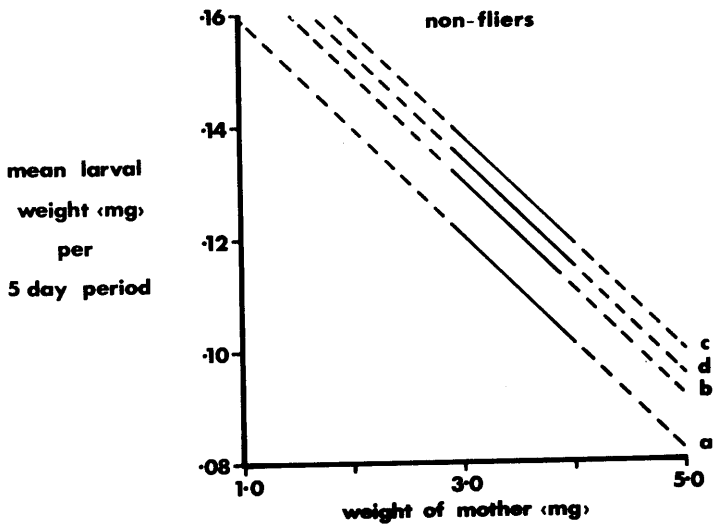

mean larval weight (mg) per 5 day period
non-fliers
·16
·14
·12
·10
·08
1·0
3·0
5·0
weight of mother (mg)
c
d
b
a

Table 9. Regression formulae and the significance of the deviation from zero of the regression coefficients for the relationships between the mean weight of individual larvae (Y) produced by apterae, fliers and non-fliers during days 1 - 5, 6 - 10, 11 - 15 and 16 - 20 of reproductive life and the weight of the mother in milligrams (X). The common regression coefficient is given for each group.

| 5 day period | No. of mothers | Regression formula | Sig. of deviation of regr. coeff. from zero | Common regr. coeff. |
|---|---|---|---|---|
| Apterae | | | | |
| 1 | 13 | Y = 0.180 - 0.011X | 0.05 | -0.00025 |
| 2 | 13 | Y = 0.109 + 0.007X | N. S. | |
| 3 | 13 | Y = 0.136 - 0.001X | N. S. | |
| 4 | 13 | Y = 0.114 + 0.004X | N. S. | |
| Fliers | | | | |
| 1 | 14 | Y = 0.114 + 0.001X | N. S. | 0.0039 |
| 2 | 14 | Y = 0.116 + 0.004X | N. S. | |
| 3 | 14 | Y = 0.072 + 0.018X | N. S. | |
| 4 | 14 | Y = 0.195 - 0.021X | N. S. | |
| Non-fliers | | | | |
| 1 | 9 | Y = 0.149 - 0.011X | N. S. | -0.0193 |
| 2 | 8 | Y = 0.153 - 0.009X | N. S. | |
| 3 | 6 | Y = 0.264 - 0.039X | 0.10 | |
| 4 | 6 | Y = 0.241 - 0.034X | 0.10 | |

Table 10. Mean weight of larvae (mg) produced during days 1 - 5, 6 - 10, 11 - 15 and 16 - 20 of reproductive life by 2.5 mg and 3.5 mg apterae, fliers and non-fliers.

| Weight of mother (mg) | Mean weight of larvae (mg) | | | |
|---|---|---|---|---|
| | Days 1 - 5 | Days 6 - 10 | Days 11-15 | Days 16-20 |
| APTERAE | | | | |
| 2.5 | 0.153 | 0.127 | 0.134 | 0.124 |
| 3.5 | 0.142 | 0.134 | 0.133 | 0.128 |
| FLIERS | | | | |
| 2.5 | 0.117 | 0.126 | 0.117 | 0.143 |
| 3.5 | 0.118 | 0.130 | 0.135 | 0.122 |
| NON-FLIERS | | | | |
| 2.5 | 0.122 | 0.131 | 0.167 | 0.156 |
| 3.5 | 0.111 | 0.122 | 0.128 | 0.122 |

Table 11. Regression formulae for the relationship between the mean weight of larvae (Y) produced by apterae, fliers and non-fliers during days 1 - 5, 6 - 10, 11 - 15 and 16 - 20 of reproductive life and the weight of the mother in milligrams (X) recalculated using the common regression coefficients from Table 9.

| | 5 day period | Regression formula using C.R.C. |
|---|---|---|
| **Apterae** | | |
| | 1 | $Y = 0.137 - 0.00025X$ |
| | 2 | $Y = 0.139 - 0.00025X$ |
| | 3 | $Y = 0.133 - 0.00025X$ |
| | 4 | $Y = 0.131 - 0.00025X$ |
| **Fliers** | | |
| | 1 | $Y = 0.108 + 0.0039X$ |
| | 2 | $Y = 0.118 + 0.0039X$ |
| | 3 | $Y = 0.115 + 0.0039X$ |
| | 4 | $Y = 0.112 + 0.0039X$ |
| **Non-fliers** | | |
| | 1 | $Y = 0.178 - 0.0193X$ |
| | 2 | $Y = 0.188 - 0.0193X$ |
| | 3 | $Y = 0.196 - 0.0193X$ |
| | 4 | $Y = 0.192 - 0.0193X$ |

11 to 15 and 16 to 20 of its reproductive life ( Table 8 ) to be an alata costs a 3.5 mg aphid roughly 10% of its larva production ( i.e. comparing non-fliers with apterae ) but use of its wings and wing muscles reduces the larva production of a 2.5 mg alata to 73.27% of that of an aptera and to 71.45% of that of an alata which does not fly. A 3.5 mg flying alata produces 81.97% of the total mass produced by an aptera of the same weight and 91.02% of that of an equivalent non-flier.

The much lower total mass of larvae produced by small flown alatae during the first ten days of reproduction is due only to the small numbers of larvae they produce ( Figure 19 ). Mean weights of larvae from both flying and non-flying alatae are similar during the first ten days ( Table 10 ). During days 1 to 5 the larvae produced by apterae are much larger ( 0.153 mg for a 2.5 mg mother and 0.142 mg for a 3.5 mg mother ) than those produced by alatae whether they fly or not. At this time there is a significant inverse relationship between mean weight of larvae of apterae and the weight of the mother ( $t = 2.394$, $d.f. = 11$, $P < 0.05$ ). During days 11 to 15 and 16 to 20 a similar relationship exists for mean larval and maternal weights of non-fliers ( 11-15; $t = 2.711$, $d.f. = 4$, $P < 0.10$ and 16-20; $t = 2.141$, $d.f. = 4$, $P < 0.10$ ).

Life tables were constructed ( Table 12 ) and the net reproduction rate, $\underline{R}_o$, was calculated for small ( 2.5 mg ) and large ( 3.5 mg ) apterae, fliers and non-fliers ( Birch, 1948 ). The survival rate ( $l_x$ ) for the immature stages is assumed to be one hundred percent for each group. Calculations were based on the numbers of young produced during each 5 day period by small and large apterae, fliers and non-fliers as estimated from the regression formulae calculated using the common regression coefficient ( Table 7 ).

The net reproduction rate which is a measure of the number of times a population with a stable age distribution will multiply itself in one generation is highest in apterae ( $\underline{R}_o$ = 75.0 for small apterae and 83.2 for large apterae ) and in non-fliers ( $\underline{R}_o$ = 74.1 for small non-fliers and 79.0 for large non-fliers ) but very much lower in fliers ( $\underline{R}_o$ = 60.9 for small fliers and 68.2 for large fliers ) ( Table 12 ).

More accurate parameters of the capacity for increase of a population are the intrinsic rate of natural increase, $\underline{r}$, which is a measure of the difference between birth and death rates in a population, and $\underline{\lambda}$ = antilog$_e\underline{r}$, which is the finite rate of increase of the population ( Birch, 1948 ). These take into account the length of time from birth to maturity, the time during which reproduction occurs and the reproductive rate.

Table 12. Life tables for populations of 2.5 mg and 3.5 mg apterae, fliers and non-fliers showing the net reproduction rate, $R_o$, for each population. Survival rates, $(l_x)$, and reproductive rates, $(m_x)$, are taken over periods of 5 days, the mid points of which time intervals are indicated by $x$.

| x | $(l_x)$ | $(m_x)$ | $(l_x m_x)$ |
|---|---|---|---|
| 2.5 mg apterae | | | |
| 0.5 | 1.0 | 0 | 0 |
| 1.5 | 1.0 | 0 | 0 |
| 2.5 | 0.95 | 28 | 26.6 |
| 3.5 | 0.90 | 23.6 | 20.7 |
| 4.5 | 0.75 | 22.0 | 16.5 |
| 5.5 | 0.70 | 16.0 | 11.2 |
| | | $R_o$ = | 75.0 |
| 3.5 mg apterae | | | |
| 0.5 | 1.0 | 0 | 0 |
| 1.5 | 1.0 | 0 | 0 |
| 2.5 | 0.95 | 30 | 28.5 |
| 3.5 | 0.90 | 25.5 | 23.0 |
| 4.5 | 0.75 | 24.5 | 18.4 |
| 5.5 | 0.70 | 19.0 | 13.3 |
| | | $R_o$ = | 83.2 |
| 2.5 mg fliers | | | |
| 0.5 | 1.0 | 0 | 0 |
| 1.5 | 1.0 | 0 | 0 |
| 2.5 | 0.95 | 22 | 20.9 |
| 3.5 | 0.85 | 19.5 | 16.6 |
| 4.5 | 0.70 | 26.5 | 18.6 |
| 5.5 | 0.40 | 12.0 | 4.8 |
| | | $R_o$ = | 60.9 |
| 3.5 mg fliers | | | |
| 0.5 | 1.0 | 0 | 0 |
| 1.5 | 1.0 | 0 | 0 |
| 2.5 | 0.95 | 28 | 26.6 |
| 3.5 | 0.85 | 26 | 22.1 |
| 4.5 | 0.70 | 23.5 | 16.5 |
| 5.5 | 0.40 | 7.5 | 3.0 |
| | | $R_o$ = | 68.2 |
| 2.5 mg non-fliers | | | |
| 0.5 | 1.0 | 0 | 0 |
| 1.5 | 1.0 | 0 | 0 |
| 2.5 | 1.0 | 30.5 | 30.5 |
| 3.5 | 0.85 | 26.0 | 22.1 |
| 4.5 | 0.67 | 23.5 | 15.7 |
| 5.5 | 0.50 | 11.5 | 5.8 |
| | | $R_o$ = | 74.1 |
| 3.5 mg non-fliers | | | |
| 0.5 | 1.0 | 0 | 0 |
| 1.5 | 1.0 | 0 | 0 |
| 2.5 | 1.0 | 32.0 | 32.0 |
| 3.5 | 0.85 | 27.5 | 23.4 |
| 4.5 | 0.67 | 25.0 | 16.8 |
| 5.5 | 0.50 | 13.5 | 6.8 |
| | | $R_o$ = | 79.0 |

The r values for fliers are not as different from those for non-fliers and apterae as could be expected from the net reproduction rates, $R_o$ ( Tables 12 and 13 ). The net reproduction rate of a population of small fliers is 81% of that of a population of small apterae and 82% of that of a population of small non-fliers. A population of large fliers has a net reproduction rate which is 82% of that of a population of large apterae and 86% of that of a population of large non-fliers ( Table 12 ). The greatest difference in intrinsic rate of natural increase is between populations of small fliers and non-fliers. The r value for small fliers is 91% of that of small non-fliers ( Table 13 ).

Fliers are capable of making good some of the net reproduction rate deficit. The percentage contribution of the individual 5 day periods towards the intrinsic rate of natural increase ( Table 14 ) indicates an explanation. During days 6 to 15 the reproductive rate of small fliers contributes 21.53% towards the value of r and that of large fliers contributes 19.49% towards r during this time ( Table 14 ). Small apterae contribute 18.75% to r during this time and large apterae 18.78%.

A population of alatae which do not fly can compensate so well for the low value of $R_o$ that the population has a much higher intrinsic rate of natural increase, r, than has a population of apterae ( Table 13 ). They produce more larvae during the first 5 days of their reproductive life and so contribute much more

Table 13. Intrinsic rates of natural increase, r, and finite rates of increase, $\lambda$, for populations, with stable age distributions, of apterae, fliers and non-fliers of different weights.

| | weight | r | $\lambda$ |
|---|---|---|---|
| Apterae | | | |
| | 2.5mg | 1.39 | 4.01 |
| | 3.5mg | 1.42 | 4.14 |
| Fliers | | | |
| | 2.5mg | 1.32 | 3.74 |
| | 3.5mg | 1.40 | 4.06 |
| Non-fliers | | | |
| | 2.5mg | 1.45 | 4.26 |
| | 3.5mg | 1.46 | 4.31 |

towards $r$ than apterae do during the same period ( Table 14 ).

Populations of small apterae and non-fliers have very nearly the same net reproduction rate, $R_o$, ( Table 12 ) and almost the same intrinsic rate of natural increase, $r$, ( Table 13 ) as populations of larger individuals. They distribute their larva production in time so that each 5 day period contributes the same percentage towards $r$ ( Table 14 ) as does the equivalent period of time for a population of the larger aphids.

Populations of small and large fliers have very different $R_o$ values ( Table 12 ) and $r$ values ( Table 13 ). Small fliers contribute only 78% towards $r$ during the first five days compared with 80.37% contributed by large fliers. The lower value of $r$ for a population of small fliers arises because they produce a much smaller proportion of their larvae during the first 5 days of reproductive life than do individuals in a population consisting of large apterae, small apterae, large non-fliers, small non-fliers or large fliers ( Figure 18 ). During days 11 to 15 small fliers produce a relatively large proportion of their offspring when compared with larger fliers ( Figure 18 ). This is reflected in the 4.96% contribution to $r$ by a population of small fliers at this time compared with 3.03% for a population of large fliers ( Table 14 ). The percentage contribution towards $r$ for large fliers is distributed over the four 5 day periods in the same

Table 14. Percentage contribution of each five day period towards r in populations of apterae, fliers and non-fliers of different weights.

| | Weight (mg) | % contribution to r | | | |
|---|---|---|---|---|---|
| | | days 1-5 | 6-10 | 11-15 | 16-20 |
| Apterae | 2.5 | 80.72 | 15.65 | 3.10 | 0.53 |
| | 3.5 | 80.69 | 15.74 | 3.04 | 0.53 |
| Fliers | 2.5 | 78.12 | 16.57 | 4.96 | 0.34 |
| | 3.5 | 80.37 | 16.46 | 3.03 | 0.13 |
| Non-fliers | 2.5 | 83.28 | 14.15 | 2.36 | 0.21 |
| | 3.5 | 83.28 | 14.14 | 2.36 | 0.22 |

way as for small and large apterae ( Table 14 ).

A population of M. viciae, apterous or alate, which remains on the original host plant can multiply in unit time much faster than a population of alatae which fly and colonise a new host ( Table 13 ).

Small alatae lose about 20% of their potential larva production if they fly ( Table 12 ). Although this is largely compensated for by the distribution in time of larva production the intrinsic rate of natural increase of a population of small fliers is much lower than those of populations of small apterae and non-fliers. Larger alatae lose only 14% of their potential larva production if they fly ( Table 12 ) and their intrinsic rate of natural increase is almost as high ( 1.40 ) as that of apterae ( 1.41 and 1.42 ) ( Table 13 ). Populations of non-fliers have a higher intrinsic rate of natural increase than those of apterae ( Table 13 ) although their net reproduction rate is lower ( Table 12 ).

Populations of alate M. viciae can reproduce themselves in unit time less often if the alatae are small and have flown ( $\lambda$ = 3.74 ) ( Table 13 ) than if they are large and have flown ( $\lambda$ = 4.06 ). In the latter case they have a finite rate of increase $\lambda$ equal to that of a population of apterae ( Table 13 ). A population of alatae which has not flown can multiply in unit

time more than a population of apterae ( Table 13 ). The physiological state of alatae is such that if a population of alatae does not fly it is capable of multiplying in unit time much faster than a population of large apterae.

## 3(g). RESPIRATION RATES

In hibernating Colorado beetles, Leptinotarsa decemlineata, respiration rate falls, 75% of this decrease being due to the degeneration of the flight muscles and their mitochondria ( Stegwee, 1964 ). In view of this and the fact that M. viciae alatae lose their wing muscles the respiration rates of fliers and non-fliers might be quite different from those of apterae and from those of each other at some stages in their lives.

The oxygen uptake / hour by individual apterae, fliers and non-fliers was measured using a capillary respirometer ( p.11 ). Aphids were respired at daily intervals from the day after moult until some days after reproduction had started and the log-log relationship between µl oxygen consumed per aphid per hour and the weight in milligrams of the aphid determined ( Table 15 ). To make comparison of the resulting regression lines possible, these were recalculated using the common regression coefficient for each of the three groups ( Figure 20, Table 16 ). The regression lines for both apterae and non-fliers at the stages studied were all similar ( $F = 2.402$, d.f. = 4/66 for non-fliers; $F = 2.438$, d.f. = 4/40 for apterae ). When the slopes of the regression lines for fliers were compared, however, that for fliers about to fly had a completely different slope from the others ( $F = 3.472$, d.f. = 7/112, P 0.01 for all lines; $F = 1.104$, d.f. = 6/99 excluding those about to fly ).

Table 15. Regression formulae for the log./log. relationship of µl oxygen consumed / animal / hour on successive days after the adult moult for apterae, fliers and non-fliers with the significance of deviation from zero slope of these lines and the common regression coefficient calculated for each group.

| Time | No. of aphids | Regression formula | Sig. of deviation of regression coeff. from zero | Common regr. coeff. |
|---|---|---|---|---|
| Apterae | | | | |
| Day after moult | 10 | Y = 0.123 + 0.974X | 0.001 | 0.972 |
| Two days after moult | 7 | Y = 0.066 + 0.915X | 0.05 | |
| 1st day of reproduction° | 17 | Y = 0.412 + 0.432X | N. S. | |
| 2nd day of reproduction | 10 | Y = 0.250 + 0.686X | 0.10 | |
| 4th day of reproduction | 6 | Y = -0.555 + 1.786X | 0.01 | |
| Fliers | | | | |
| Day after moult | 10 | Y = 0.100 + 1.103X | 0.001 | 0.726 |
| About to fly* | 15 | Y = -0.070 + 1.731X | 0.001 | |

* not included in estimate of common regression coefficient

Table(15 cont.)

| Time | No. of aphids | Regression formula | Sig. of deviation of regr. coeff. from zero | Common regr. coeff. |
|---|---|---|---|---|
| Fliers(cont.) | | | | |
| One day after settling | 19 | Y = 0.068 + 0.968X | 0.001 | 0.726 |
| 2 days after settling* | 17 | Y = 0.263 + 0.523X | 0.02 | |
| 3 days after settling | 23 | Y = 0.163 + 0.662X | 0.01 | |
| 4 days after settling | 11 | Y = 0.330 + 0.535X | N. S. | |
| 5 days after settling | 21 | Y = 0.458 + 0.304X | N. S. | |
| 6 days after settling | 12 | Y = 0.296 + 0.680X | 0.05 | |
| Non-fliers | | | | |
| Day after moult | 14 | Y = 0.013 + 0.952X | 0.05 | 0.915 |
| Two days after moult | 15 | Y = 0.239 + 0.728X | 0.05 | |
| 1st day of reproduction | 22 | Y = -0.125 + 1.400X | 0.001 | |

* 1st day of reproduction

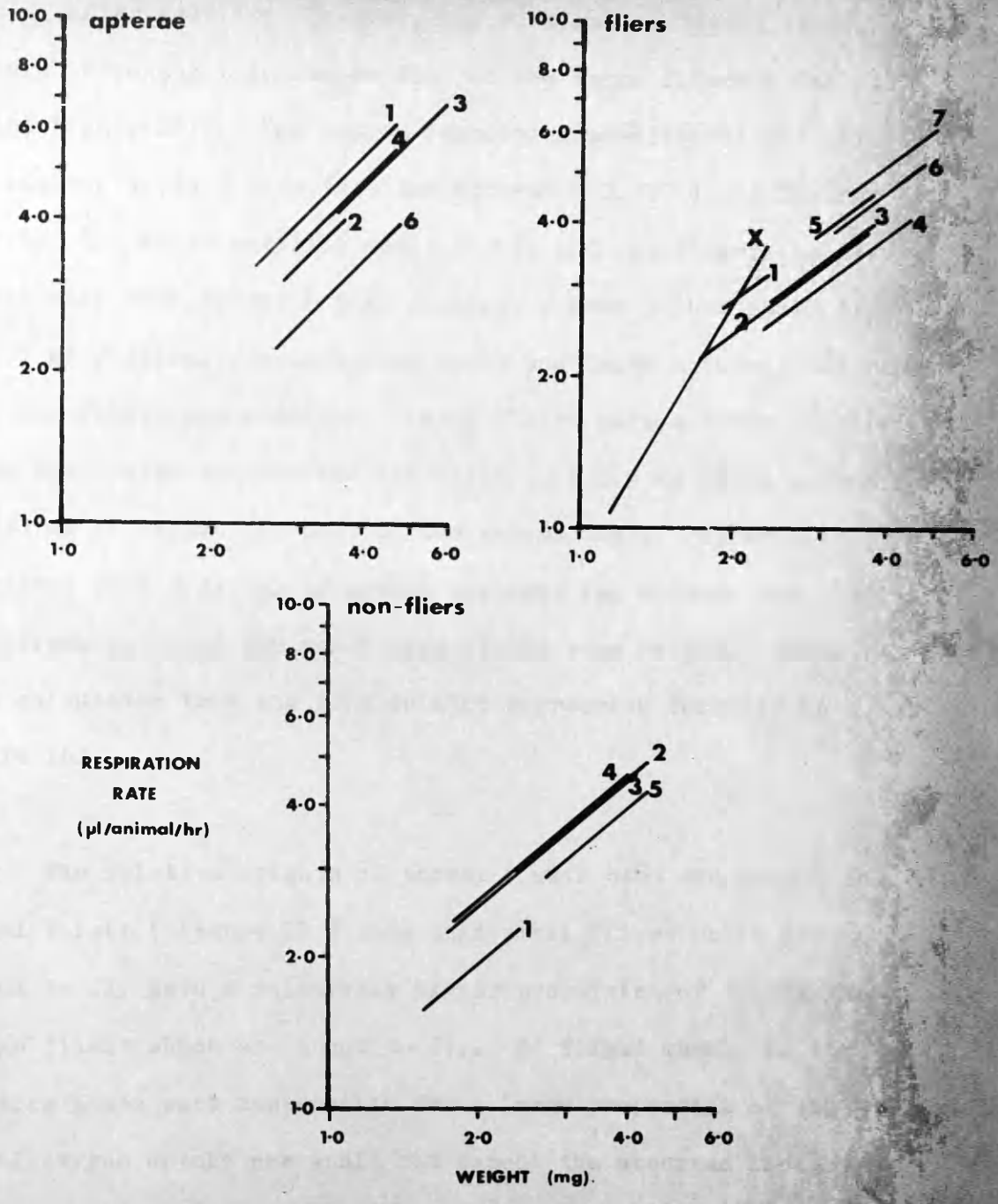
Table 15 (cont.)

| Time | No of aphids | Regression formula | Sig. of deviation of regr. coeff. from zero | Common regr. coeff. |
|---|---|---|---|---|
| Non-fliers ( cont. ) | | | | |
| 2nd day of reproduction | 12 | Y = 0.254 + 0.704X | 0.001 | 0.915 |
| 3rd day of reproduction | 13 | Y = 0.301 + 0.490X | N. S. | |

Table 16. Recalculated regression formulae using the common regression coefficients from Table 15 for the relationship between µl oxygen consumption / whole animal / hour and the weight of the animal (mg) for apterae, fliers and non-fliers.

| Time | Recalculated regression formula using the C.R.C. |
|---|---|
| **Apterae** | |
| Day after moult | Y = 0.124 + 0.972X |
| Two days after moult | Y = 0.038 + 0.972X |
| 1st day of reproduction | Y = 0.061 + 0.972X |
| 2nd day of reproduction | Y = 0.075 + 0.972X |
| 4th day of reproduction | Y = -0.079 + 0.972X |
| **Fliers** | |
| Day after moult | Y = 0.230 + 0.726X |
| 1 day after settling | Y = 0.172 + 0.726X |
| 2 days after settling | Y = 0.163 + 0.726X |
| 3 days after settling | Y = 0.129 + 0.726X |
| 4 days after settling | Y = 0.231 + 0.726X |
| 5 days after settling | Y = 0.218 + 0.726X |
| 6 days after settling | Y = 0.269 + 0.726X |
| **Non-fliers** | |
| Day after moult | Y = 0.024 + 0.915X |
| Two days after moult | Y = 0.149 + 0.915X |
| 1st day of reproduction | Y = 0.499 + 0.915X |
| 2nd day of reproduction | Y = 0.148 + 0.915X |
| 3rd day of reproduction | Y = 0.076 + 0.915X |

Figure 20. Respiration rates measured as µl $O_2$ / whole animal / hour plotted against weight of the animal in milligrams for apterae during days 1 - 4 and 6 ( 1 - 4 and 6 on graph ) after the adult moult, for fliers on day 1 ( 1 on graph ) after moult, on days 1 - 6 ( 2 - 7 on graph ) after settling and during the excited preflight phase ( x on graph ) and for non-fliers on days 1 - 5 ( 1 - 5 on graph ) after moult.

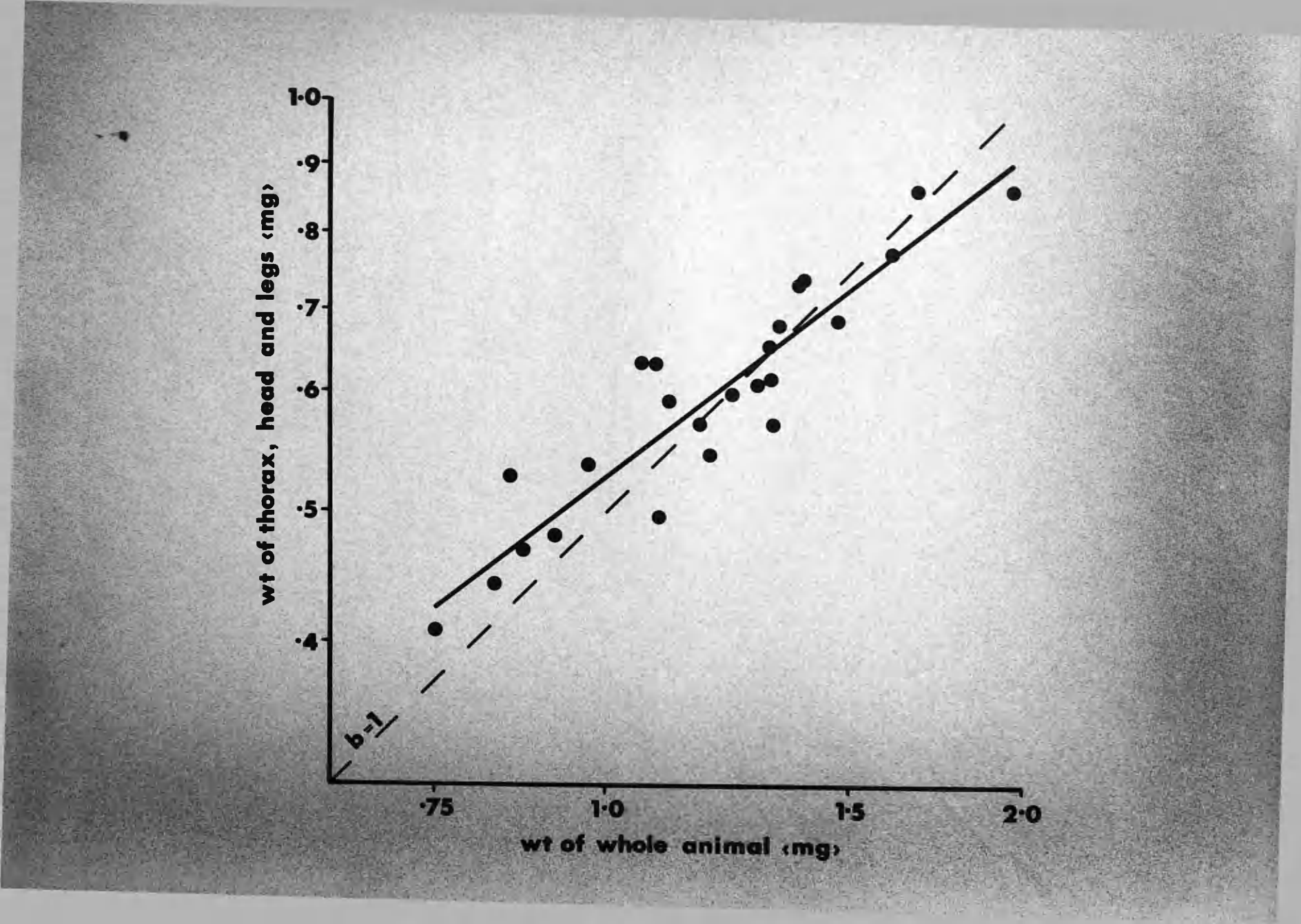

apterae
fliers
non-fliers
10·0
8·0
6·0
4·0
2·0
1·0
1·0
2·0
4·0
6·0
RESPIRATION
RATE
(µl/animal/hr)
WEIGHT (mg).

When they are about to take off from the plant small fliers have a relatively much lower respiration rate than large fliers ( Figure 20 ). After settling, however, the respiration rate of small fliers increases relative to that of the large fliers ( Tables 15 & 16, Figure 20 ). The common regression coefficient for fliers is lower ( 0.726 ) than that for apterae ( 0.972 ) and for non-fliers ( 0.915 ). After settling small fliers and non-fliers are respiring relatively much faster ( 2 µl / animal / hour ) than small apterae ( 1.7 µl / animal / hour ) when small and large apterae, fliers and non-fliers are compared. Large fliers have a lower respiration rate than large apterae and non-fliers. A 3.5 mg flier consumes 2.670 µl of oxygen per hour on the second day of reproduction compared with 3.477 µl of oxygen per hour for apterae and 3.351 µl of oxygen per hour for non-fliers of the same weight. These values are calculated from the recalculated regression formulae in Table 16.

The relative weights of thorax ( with head and legs ) and total weight ( Figure 21 ) show that small fliers which are about to fly have a relatively higher proportion of thorax than large fliers which are about to fly. If flight muscle in its resting state were responsible for a large proportion of the total oxygen uptake one would not expect the observed increase in slope of the respirometry curve for fliers about to fly ( Figure 20 ).

Figure 21. Weight ( mg ) of thorax, head and legs of fliers about to fly plotted against weight ( mg ) of the whole animal.

( $b = 0.768$, $P < 0.01$ for comparison with $b = 1$ )


1·0
·9
·8
·7
·6
·5
·4
wt of thorax, head and legs (mg)
b=1
·75
1·0
1·5
2·0
wt of whole animal (mg)

The only factor which could so drastically affect the respiration rate of alatae which are about to fly is embryogenesis. Large alatae about to fly have larger abdomens and thus contain more embryos than small alatae ( Figure 21 ). The higher respiration rate of these large fliers is probably due either to the presence of more embryos already formed or to the continuing formation of embryos which for some reason is slowed down or stopped in the small fliers. The oogenesis flight syndrome applies to small fliers rather than large. This decline in the rate of embryo formation may be responsible for the small number of larvae produced by small fliers during the first ten days of reproductive life ( Figure 18 ).

Small fliers whose embryo production is slowed down or stopped could be described as highly migratory according to the oogenesis flight syndrome. Large fliers whose embryo development continues during the pre-flight wandering over the plant ( and perhaps during flight ) could be described as intermediate between sensori-motor and vegetative phases. Both large and small fliers, however, are migratory in behaviour. A large flier has the ability to undertake a migratory flight and still support embryo development.

It is interesting that after the second day of reproduction the respiration rates for apterae and non-fliers shows a general fall whereas for fliers it is still rising at this time ( Figure 20 ).

This may reflect an increase in embryogenesis which is delayed in fliers as a result of flying and which has reached its peak in apterae and non-fliers before reproduction starts.

In sycamore aphid, Drepanosiphum platanoides, virginoparae emerging from diapause were found to have a higher respiration rate than their daughters ( McNaughton, 1971 ). This increase in oxygen uptake was probably a result of increased embryogenesis after diapause.

Respiration rates reflect differences in reproductive capacity of apterae, fliers and non-fliers rather than differences arising from the resting metabolism of intact or degenerating flight muscles.

## 3(h). ALATA PRODUCTION BY ALATAE

Alate virginoparae of M. viciae and other aphid species ( Wadley, 1923; Reinhard, 1927; Bonnemaison, 1951; Noda, 1959; MacGillivray & Anderson, 1964; Hille Ris Lambers, 1966; Lees, 1966; Sutherland, 1970 ) are less likely to produce alate offspring than apterous. In none of these studies has any distinction been made between alatae which fly and those which do not. Only in A. pisum ( Sutherland, 1970 ) have more than one type of alatae been considered and here the difference is between alatae of a pink strain and alatae of a green strain where those of the pink strain produce alatae more readily.

Since alate virginoparae can behave like apterae by being flightless it is possible that they are similar to apterae in other ways. One of the most clear-cut differences between apterae and alatae of M. viciae, apart from the possession of wings and the ability to fly, is that alata production is inhibited in alate virginoparae ( Lees, 1966 ). Also, if an alata does not fly but remains in the original colony, it would be advantageous for it to produce alate daughters in the same way as an apterous individual.

Two generations of apterae were reared in isolation. When the second became adult they were crowded using the standard method ( p. 8 ) for 24 hours so that the resulting offspring

would include alatae. All of this third generation were reared in isolation until the fourth instar when some of the alatae were crowded by placing 30 third instar larvae on each seedling. Those which flew were allowed to settle on new plants without being handled.

Fliers, non-fliers and apterae which had reproduced for one day were given the standard crowding treatment ( p.8 ) in a specimen tube for 24 hours. They were afterwards returned singly to fresh bean seedlings and left to reproduce for three days before being removed. When the resulting larvae reached the adult stage the numbers of apterous and alate virginoparae and males produced by each of the mothers was noted. The proportions of alate and apterous offspring are not influenced by rearing conditions since alata determination in M. viciae acts only through the mother ( Lees, 1961 ).

The results are shown in Table 17. The means of the total numbers of larvae produced in three days ( 24.8, 21.4 and 27.6 for apterae, fliers and non-fliers respectively ) are comparable to, but higher than, the average numbers produced during the same three days by the animals used to measure reproductive rates etc. ( 16.32, 12.39 and 17.64 for apterae, fliers and non-fliers respectively ). The increased numbers here are probably because no larvae were produced when the mothers were in the specimen tubes.

Table 17. Number and morphs of progeny of apterae, fliers and non-fliers after a period of 24 hours of crowding in groups of 10 in a 2.5 cm x 5.0 cm specimen tube.

| | APTERAE | | | | | FLIERS | | | | | NON-FLIERS | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ident. | Tot. | Al. | Apt. | Males | %Al. | Tot. | Al. | Apt. | Males | %Al. | Tot. | Al. | Apt. | Males | %Al. |
| 1 | 28 | 23 | 5 | 0 | 82.1 | 22 | 0 | 22 | 0 | 0 | 37 | 9 | 26 | 2 | 24.0 |
| 2 | * 2 | 0 | 2 | 0 | 0 | 21 | 0 | 21 | 0 | 0 | 35 | 5 | 30 | 0 | 14.3 |
| 3 | 29 | 11 | 17 | 1 | 37.9 | * 7 | 0 | 7 | 0 | 0 | 29 | 3 | 26 | 0 | 10.3 |
| 4 | 32 | 16 | 16 | 0 | 50.0 | 17 | 0 | 17 | 0 | 0 | 19 | 7 | 10 | 2 | 36.8 |
| 5 | 20 | 6 | 14 | 0 | 30.0 | 17 | 2 | 15 | 0 | 11.8 | 27 | 0 | 27 | 0 | 0 |
| 6 | 34 | 2 | 31 | 1 | 5.9 | * 6 | 0 | 6 | 0 | 0 | 28 | 1 | 27 | 0 | 3.6 |
| 7 | 35 | 10 | 21 | 4 | 28.6 | * 1 | 0 | 1 | 0 | 0 | 30 | 5 | 25 | 0 | 16.7 |
| 8 | 24 | 0 | 24 | 0 | 0 | *11 | 0 | 11 | 0 | 0 | 36 | 16 | 19 | 1 | 44.4 |
| 9 | 28 | 0 | 28 | 0 | 0 | * 5 | 0 | 5 | 0 | 0 | * 2 | 1 | 1 | 0 | 50.0 |

Table 17 (continued).

| | APTERAE | | | | | FLIERS | | | | | NON-FLIERS | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ident. | Tot. | Al. | Apt. | Males | %Al. | Tot. | Al. | Apt. | Males | %Al. | Tot. | Al. | Apt. | Males | %Al. |
| 10 | 25 | 0 | 24 | 1 | 0 | *13 | 0 | 12 | 1 | 0 | 34 | 18 | 16 | 0 | 52.9 |
| 11 | *10 | 1 | 9 | 0 | 10.0 | 26 | 0 | 26 | 0 | 0 | 26 | 5 | 21 | 0 | 19.2 |
| 12 | 17 | 8 | 8 | 1 | 47.1 | 24 | 1 | 23 | 0 | 4.2 | 20 | 0 | 20 | 0 | 0 |
| 13 | 10 | 2 | 8 | 0 | 20.0 | 21 | 0 | 21 | 0 | 0 | 19 | 9 | 8 | 2 | 47.4 |
| 14 | 15 | 0 | 15 | 0 | 0 | 23 | 0 | 22 | 1 | 0 | 19 | 0 | 19 | 0 | 0 |
| 15 | | | | | | | | | | | 27 | 2 | 24 | 1 | 7.4 |
| Mean | 24.8 | | | | 22.3 | 21.4 | | | | 1.1 | 27.6 | | | | 21.8 |

* Mother died or left plant before 3 days had elapsed.

Mean of Tot. column taken only from animals surviving for 3 days.

Non-flying alatae produce more alatae ( 21% ) than those which fly ( 1.1% ) and in numbers of the same order as apterae ( 22.3% ). Apterae and non-fliers produced more males than the flying alatae.

There is a great deal of variation in the response of apterae and non-fliers to crowding. Because of this the terms "aptera-producer" and "alata-producer" as used by Lees ( 1967 ) and Sutherland ( 1970 ) have not been used here. These terms imply an all-or-nothing response and seem totally unsuitable in the case of M. viciae where the percentage of alatae produced varies from 0 to 82.1 in apterae and from 0 to 52.9 in non-fliers. Lees ( 1967 ) found a similar randomness in response when apterae were reared in isolation from the third larval instar and then, three days after the adult moult, crowded for 24 hours in a specimen tube. He reared two lines for 20 generations, one where "aptera-producers" were used as parents and the other where "alata-producers" were used as parents. Both lines originated from a single alata. The percentage of "alata-producers" varied randomly from generation to generation ( Lees, 1967 ). The variation in the results reported here ( Table 17 ) and by Lees ( 1967 ) could be due to several factors. There may have been differences in the plants which an experimenter could not detect. Small variations in the age or rate of development of the aphids could affect their response to a crowding stimulus. Aphids may receive quite different amounts of

stimulation while in the specimen tube. The more active aphids will come into contact with other aphids much more often than those which do not move around much. This could well be the main reason for the great differences in response.

Inhibition of alata production in an alata M. viciae arises only if the alata is excited to flight.

## 4. DISCUSSION

It has been shown that alatae of M. viciae can respond to current adverse conditions when they fly after the adult moult. Crowding during larval life and the crowding experience of previous generations do affect numbers flying but these factors are outweighed by the effect of crowding experienced at the time of adult moult ( Figure 8 ).

There appear to be two components in the flight behaviour of M. viciae. The most important is the ability to respond to current conditions at the time of flight so that should conditions be favourable an alata will remain on the original plant. Secondly, there are the modifying effects of larval experience of the alata and the experience of previous generations.

It has been claimed that in Aphis fabae larval and maternal experience are entirely responsible for the flight behaviour of alatae when they become adult ( Shaw, 1970c ). If conditions have been unfavourable for the mother or during the early larval life of the alata, the alata is said to be a "migrant" with an irrepressible urge to fly as soon as it becomes adult. In more favourable conditions larger alatae, "fliers" which have a less compelling "migratory urge" and which deposit some larvae before they fly, and "non-fliers" which have no "migratory urge" arise.

The behaviour, as well as morphology and physiology, of A. fabae alatae is thought to be ontogenetically determined ( Shaw, 1970c ).

It has been suggested ( Johnson, 1969; Shaw, 1970c ) that an ontogenetic theory to explain flight behaviour can be extended to other aphid species. Such a hypothesis cannot explain the flight behaviour of Megoura viciae. The present work suggests, however, that there may be both ontogenetic and immediate behavioural components of the flight behaviour of aphids. In M. viciae the current response to adversity greatly outweighs any ontogenetic factors and these serve only to modify the response. In A. fabae because the morphology of alatae is affected by larval experience some alatae may have incomplete wings or wing muscles and be unable to fly. Those which Shaw has called "migrants", however, may be susceptible to current environmental stimuli but with a very high threshold of response. It may also be possible to make "non-fliers" of A. fabae fly by crowding them prior to adult moult.

Another aphid species which is very like M. viciae in several ways is Acyrthosiphon pisum. Alatae arise, like those of M. viciae, as a result of crowding of the mother ( Sutherland, 1969 ) and in the pink strain alatae will produce alate daughters. Alatae of the pink strain may then be capable of responding to current conditions by flying or not.

Structurally all alatae of M. viciae are the same. Even

those which do not fly when they are isolated have complete wing musculature ( p.24 ). Muscle breakdown does not begin until at least twelve hours after moult even in those which do not fly ( p.26 ).

The mechanism of muscle breakdown operates very rapidly ( p.27 ) and so is probably hormonal in nature and triggered by changes in nervous output to the muscle as in the intersegmental muscles of the moth, Antheraea pernyi ( Lockshin & Williams, 1965b, 1964 ). Degeneration simply as a result of cessation of nervous information to the muscle without a specially primed hormone system to actively break up the muscle would take much longer than seven days. Denervation of locust retractor unguis muscle resulted in 20% of the muscle still remaining after 70 days ( Rees, 1971 ). In M. viciae 50% of the indirect flight muscle fibril volume is lost within two days after settling in fliers and 75% between 48 and 72 hours after adult moult in non-fliers ( Figure 17 ). This would only be possible with a breakdown system similar to that in A. pernyi.

An alata which flies goes through an excited phase during which it becomes very active on the plant, finds a high point and takes off. Between moult and flight an average flier loses 20% of its live weight as water ( p.20, Figure 10 ) probably because the animal does not feed and evaporation losses are not made good.

It has been thought that flight is a prerequisite for settling in aphids. Work on settling responses of A. fabae after tethered and untethered flights of different durations showed that the longer the flight the more likely an aphid was to settle and that flights as short sa a few seconds were enough to make migratory aphids settle temporarily ( Johnson, 1954; Kennedy & Booth, 1963a,b ). It is much more likely that flight is a prerequisite for settling in an aphid which is in the excited phase prior to flight and in an aphid which has not been stimulated by the environment ( at any time ) to fly, flight does not have to occur for the aphid to lead a normal life. If A. fabae has a high threshold of response to current conditions at the time of flight then one would expect flight in A. fabae to be essential for an alata to settle and reproduce.

Alatae which do not fly are like apterae in more ways than just being flightless. Isolated non-fliers and isolated fliers move around on a plant very little but on heavily infested bean plants they wander around and within a few days will walk off the plant. Thus apterae and alatae alike respond to current crowding by leaving the plant.

A population of non-fliers has almost the same net reproduction rate, $R_o$, as, and a very much higher intrinsic rate of natural increase than a population of even the largest apterae ( Tables 12 & 13 ). Alatae are thus potentially as representative as apterae

are of the vegetative phase of the oogenesis flight syndrome. If they fly, however, small alatae sacrifice some 20% of their potential progeny ( p.36 ). The intrinsic rate of natural increase of a population of small alatae which have flown is much lower than that estimated for populations of small apterae. A population of large fliers, although made up of individuals less fecund than apterae ( Table 12 ) has an intrinsic rate of natural increase equivalent to that of an apterous population. The difference in "migratory urge" between "migrants" and "fliers" in A. fabae ( Shaw, 1970b ) may be similar to the difference between small and large fliers of M. viciae i.e. a difference in reproductive capacity as suggested by Dixon ( 1971 ). A. fabae "migrants" which fly without producing larvae may have a reduced rate of embryo production for the same reasons as do small M. viciae fliers.

Respiration rates for alatae after flight tend to increase on successive days. In apterae and non-fliers the tendency is for whole animal respiration rates to fall after the second day after moult. This indicates that the peak of embryogenesis may be delayed in fliers, especially in small individuals, until after flight. In B. brassicae newly moulted alatae have a higher respiration rate than newly moulted apterae and once reproduction has started the respiration rate of alatae falls until it is lower than that of apterae ( Dixon & Flannigan, manuscript ). This is probably also a reflection of increased embryogenesis in alatae after flight. In apterae and non-fliers embryogenesis continues

without the interruption of flight and by two days after moult the peak of embryo development is over.

Smaller alatae pay a much greater price for flight in terms of reproductive capacity than larger alatae do. A 2.5 mg alata loses 27% of its potential larva production when measured as biomass, whereas a 3.5 mg flier loses only 9% of its potential larva production.

Small fliers produce relatively few embryos during the first 5 days of reproduction. They have relatively smaller abdomens than large fliers just prior to flight and at this time their respiration rate, which reflects the rate of embryo development, is relatively much lower than that of small non-fliers and apterae ( Figure 20 ). All fliers lose the same weight of water between moult and flight so that an alata weighing 1.5 mg at moult will lose 33% of its weight in water before flight and an alata weighing 2.0 mg at moult will lose 20% of its weight in water. There is no evidence for supposing that small fliers are more active than large fliers between adult moult and take-off. The respiration rate of small fliers is very low at this time. One would not expect this if they were moving around more than the larger alatae. Evaporation through the spiracles could be responsible for a large amount of water loss. This would not vary with the size of aphid since all aphids have the same number of spiracles. Some water may be lost through the body surface especially just after moult

before the cuticle has hardened. The greater dehydration suffered by small fliers may be responsible for the slowing down of embryogenesis.

Inhibition of alata production in alate mothers of M. viciae ( Lees, 1966 ) occurs only in an alata which has flown. Presumably flight inhibits the release of the substance from the central nervous system which is thought to affect alata production via the corpus allatum ( Johnson & Birks, 1960; Lees, 1966 ). It would be of no advantage to a non-flying alata remaining in the original colony not to be able to produce alate offspring. The fact that it is an alata probably means that the colony has been on the same plant for several generations and the chances of adverse conditions arising will be very high.

The comparison of aspects of the life of flying and non-flying alatae and apterae of M. viciae shows that reduced reproductive capacity, the necessity for flight before settling and the nature of resulting offspring are all characteristic of an alata which has been excited to fly and not, as was previously thought, characteristic of all alatae. Alatae which do not fly resemble apterae in all respects save the possession of wings.

## 5. SUMMARY

1. The vetch aphid Megoura viciae Buckton was used to determine whether a previously proposed ontogenetic theory to explain migration in aphids was applicable to a species other than that used for the original formulation of the theory

2. The flight behaviour of M. viciae reared in different regimes of isolation and crowding was investigated. Crowding at time of adult moult and during the teneral period was found to cause a larger proportion of the alatae to fly than if alatae were isolated from other aphids at this time. Larval and maternal experience of crowding modify the response of the alatae to current conditions at the time of flight.

3. The condition of the indirect flight muscles of alatae which fly and alatae which do not fly was studied by light microscope methods. Non-flying alatae have intact wing muscles at least up to twelve hours after the adult moult.

4. Alatae which do not fly produce more larvae than those which do fly. A population of alatae which have not flown has a higher intrinsic rate of natural increase than a population of even the largest apterae.

5. Respiration rates reflect the rate of embryo development in apterae, fliers and non-fliers of M. viciae, rather than the presence or absence of flight muscles.

6. Flight in alatae of M. viciae inhibits the production of alate offspring.

7. It is concluded that there are both ontogenetic and immediate behavioural components of the flight behaviour of alatae of M. viciae. Alatae which do not fly are like apterae in all respects save the possession of wings.

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APPENDIX 1.

Table 1. Percentage alate progeny of the mother apterae, the total number of alatae used in each experiment and the percentage of alatae which flew as adults after being isolated from birth to the time of flight.

| % alate progeny of mother apterae | total alatae | % fliers |
|---|---|---|
| 55.0 | 9 | 11.1 |
| 54.5 | 30 | 40.0 |
| 52.9 | 27 | 26.0 |
| 24.4 | 10 | 40.0 |
| 35.5 | 11 | 27.3 |
| 22.5 | 7 | 28.6 |
| 50.0 | 19 | 26.3 |
| 9.4 | 8 | 50.0 |
| 57.1 | 17 | 31.3 |
| 31.3 | 25 | 42.5 |
| 21.5 | 13 | 30.0 |
| 13.9 | 4 | 0 |
| 37.5 | 9 | 44.4 |
| 13.9 | 5 | 40.0 |
| 58.3 | 14 | 42.9 |

Table 2. Percentage alate progeny of the mother apterae and the percentage of the alatae which flew as adults after being crowded at different densities until the fourth instar and then isolated.

| % alate progeny of mother apterae | % fliers | size of crowd |
|---|---|---|
| 45.0 | 27.8 | 5 |
| 32.5 | 53.8 | 10 |
| 32.5 | 63.6 | 40 |
| 28.6 | 0 | 28 |
| 40.7 | 54.5 | 27 |
| 45.8 | 54.5 | 24 |
| 30.0 | 50.0 | 20 |
| 20.0 | 50.0 | 20 |
| 31.7 | 39.1 | 23 |
| 21.7 | 43.5 | 23 |
| 9.4 | 50.0 | 100 |
| 9.4 | 21.4 | 60 |
| 22.5 | 18.2 | 100 |
| 49.6 | 52.6 | 80 |

Table 3. Percentage alate progeny of the mother apterae and the percentage of the alatae which flew as adults after being isolated until the fourth instar and then crowded at different densities.

| % alate progeny of mother apterae | % fliers | size of crowd |
|---|---|---|
| 9.4 | 100 | 100 |
| 52.3 | 61.1 | 5 |
| 52.3 | 63.2 | 10 |
| 52.3 | 78.9 | 20 |
| 57.1 | 83.3 | 30 |
| 57.1 | 75.0 | 60 |
| 31.7 | 58.6 | 29 |
| 49.6 | 75.0 | 50 |

Table 4. Percentage alate progeny of the mother apterae and the percentage of alatae which flew as adults after being crowded at different densities from first instar until the time of flight.

| % alate progeny of mother alatae | % fliers | size of crowd |
|---|---|---|
| 64.8 | 86.7 | 20 |
| 64.8 | 100 | 20 |
| 64.8 | 50.0 | 5 |
| 63.1 | 93.7 | 42 |
| 69.4 | 94.1 | 49 |
| 76.4 | 83.1 | 55 |
| 51.1 | 77.0 | 45 |
| 18.5 | 40.0 | 27 |
| 52.0 | 77.0 | 25 |
| 55.0 | 73.0 | 20 |
| 60.0 | 94.4 | 30 |
| 36.7 | 63.6 | 30 |
| 9.4 | 100 | 60 |
| 42.1 | 100 | 52 |
| 42.1 | 84.6 | 31 |
| 42.1 | 53.8 | 31 |
| 22.5 | 100 | 100 |
| 49.6 | 87.2 | 80 |

## APPENDIX 2.

### Key

Key to case numbers in "Comparison of" column in Tables 1 & 2.

### Case

| | |
|---|---|
| 1 | Apterae days 1 - 5 |
| 2 | Apterae days 6 - 10 |
| 3 | Apterae days 11 - 15 |
| 4 | Apterae days 16 - 20 |
| 5 | Fliers days 1 - 5 |
| 6 | Fliers days 6 - 10 |
| 7 | Fliers days 11 - 15 |
| 8 | Fliers days 16 - 20 |
| 9 | Non-fliers days 1 - 5 |
| 10 | Non-fliers days 6 - 10 |
| 11 | Non-fliers days 11 - 15 |
| 12 | Non-fliers days 16 - 20 |

Table 1. F-values, degrees of freedom and the significance of separation of the regression lines for the mean weight of larvae produced by apterae, fliers and non-fliers in days 1 - 5, 6 - 10, 11 - 15 and 16 - 20 of reproductive life when each pair of lines is calculated using the common regression coefficient.

| Comparison of | Common regr.coeff. | F | d.f. | Significance at 5% |
|---|---|---|---|---|
| 1 & 2 | -0.002 | 0.436 | 1/23 | (N.S.) |
| 1 & 3 | -0.006 | 1.452 | 1/23 | (N.S.) |
| 1 & 4 | -0.004 | 3.316 | 1/23 | (N.S.) |
| 2 & 3 | +0.003 | 3.004 | 1/23 | (N.S.) |
| 2 & 4 | +0.005 | 6.184 | 1/23 | Sig. |
| 3 & 4 | +0.001 | 0.249 | 1/23 | (N.S.) |
| 5 & 6 | +0.003 | 5.087 | 1/25 | Sig. |
| 5 & 7 | +0.007 | 0.927 | 1/22 | (N.S.) |
| 5 & 8 | -0.002 | 0.858 | 1/18 | (N.S.) |
| 6 & 7 | +0.009 | 0.339 | 1/22 | (N.S.) |
| 6 & 8 | 0 | 0.412 | 1/18 | (N.S.) |
| 7 & 8 | +0.007 | 0.100 | 1/15 | (N.S.) |
| 9 & 10 | -0.010 | 2.402 | 1/14 | (N.S.) |
| 9 & 12 | -0.017 | 2.279 | 1/12 | (N.S.) |
| 10 & 11 | -0.023 | 1.369 | 1/11 | (N.S.) |
| 10 & 12 | -0.021 | 0.285 | 1/11 | (N.S.) |
| 11 & 12 | -0.036 | 0.308 | 1/9 | (N.S.) |
| 1 & 5 | -0.003 | 9.877 | 1/24 | Sig. |
| 2 & 6 | +0.005 | 0.443 | 1/24 | (N.S.) |

Table 1 (continued).

| Comparison of | Common regr.coeff. | F | d.f. | Significance at 5% |
|---|---|---|---|---|
| 3 & 7 | +0.009 | 0.073 | 1/21 | (N.S.) |
| 4 & 8 | -0.004 | 0.686 | 1/17 | (N.S.) |
| 1 & 9 | -0.011 | 25.151 | 1/19 | Sig. |
| 2 & 10 | +0.002 | 8.369 | 1/18 | Sig. |
| 3 & 11 | -0.012 | 1.116 | 1/16 | (N.S.) |
| 4 & 12 | -0.007 | 0.871 | 1/16 | (N.S.) |
| 5 & 9 | -0.003 | 0.637 | 1/20 | (N.S.) |
| 6 & 10 | +0.002 | 1.662 | 1/19 | (N.S.) |
| 7 & 11 | +0.003 | 0.031 | 1/14 | (N.S.) |
| 8 & 12 | -0.027 | 0.318 | 1/10 | (N.S.) |

(Refer to key for case numbering)

Table 2. F-values, degrees of freedom and the significance of separation of the regression lines for numbers of larvae produced by apterae, fliers and non-fliers in days 1 - 5, 6 - 10, 11 - 15 and 16 - 20 of reproductive life when each pair of lines is calculated using the common regression coefficient.

| Comparison of | Common regr.coeff. | F | d.f. | Significance at 5% |
|---|---|---|---|---|
| 1 & 2 | +0.887 | 4.673 | 1/23 | Sig. |
| 1 & 3 | +1.041 | 8.305 | 1/23 | Sig. |
| 1 & 4 | +2.620 | 36.526 | 1/23 | Sig. |
| 2 & 3 | +0.914 | 0.148 | 1/23 | (N.S.) |
| 2 & 4 | +2.492 | 9.436 | 1/23 | Sig. |
| 3 & 4 | +2.647 | 8.934 | 1/23 | Sig. |
| 5 & 6 | +6.119 | 1.333 | 1/25 | (N.S.) |
| 5 & 7 | +2.953 | 0.001 | 1/20 | (N.S.) |
| 5 & 8 | +6.307 | 60.265 | 1/18 | Sig. |
| 6 & 7 | +1.790 | 0.833 | 1/20 | (N.S.) |
| 6 & 8 | +4.850 | 40.697 | 1/18 | Sig. |
| 7 & 8 | -2.822 | 34.453 | 1/13 | Sig. |
| 9 & 10 | +4.727 | 4.708 | 1/13 | Sig. |
| 9 & 11 | +1.686 | 8.923 | 1/11 | Sig. |
| 9 & 12 | +3.386 | 75.552 | 1/10 | Sig. |
| 10 & 11 | +0.177 | 1.297 | 1/11 | (N.S.) |
| 10 & 12 | +1.666 | 51.704 | 1/10 | Sig. |
| 11 & 12 | -2.276 | 42.980 | 1/8 | Sig. |
| 1 & 5 | +5.079 | 0.173 | 1/24 | (N.S.) |
| 2 & 6 | +3.809 | 0 | 1/24 | (N.S.) |
| 3 & 7 | -2.107 | 0.688 | 1/19 | (N.S.) |

Table 2 (continued).

| Comparison of | Common regr.coeff. | F | d.f. | Significance at 5% |
|---|---|---|---|---|
| 4 & 8 | +3.822 | 7.287 | 1/17 | Sig. |
| 1 & 9 | +2.589 | 1.057 | 1/18 | (N.S.) |
| 2 & 10 | +1.540 | 0.422 | 1/18 | (N.S.) |
| 3 & 11 | -0.175 | 0.050 | 1/16 | (N.S.) |
| 4 & 12 | +3.089 | 2.196 | 1/15 | (N.S.) |
| 5 & 9 | +6.848 | 4.424 | 1/19 | Sig. |
| 6 & 10 | +4.911 | 1.744 | 1/19 | (N.S.) |
| 7 & 11 | -4.617 | 0.534 | 1/12 | (N.S.) |
| 8 & 12 | +1.368 | 3.658 | 1/9 | (N.S.) |

(Refer to key for case numbering)