SOME FACTORS AFFECTING FLIGHT ACTIVITY IN INDIVIDUAL MILKWEED BUGS (ONCOPELTUS)

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INTRODUCTION

Flight activity in the large milkweed bug, Oncopeltus fasciatus (Dallas) (Heteroptera: Lygaeidae), measured as a function of mean flight duration, is strongly influenced by age (Dingle, 1965). At 8–10 days after the final moult there occurs in both sexes a distinct peak of flight activity; in males, only, a second peak is present at 30–35 days. There are also other differences between the sexes. The 8–10 day flight peak is correlated with the end of cuticle growth, as measured by the deposition of daily cuticular growth rings, and thus represents a post-teneral phenomenon (Johnson, 1963, 1965). Because this period of maximum flight duration is post-teneral, pre-reproductive, and several times the mean duration usually observed, it was concluded that it in fact represents migration in Oncopeltus. The later activity of males was viewed as a possible later migration arising from non-migratory flights.

In addition to the above there were also indications that virgin males exhibited greater flight activity than ‘normal’ individuals not deprived of sexual partners. The data did not indicate enhanced activity for virgin females. For each sex, however, only one age-group was tested; the results, therefore, were not conclusive. Further, there was a suggestion that a behavioural polymorphism might be present. Although bugs were usually tested only once each, some were later tested again. Those which did not fly initially did not do so on later trials either, but those which did fly initially frequently flew repeatedly. To gain a more comprehensive understanding of flight activity in Oncopeltus, especially as it related to migration, it seemed worth while to explore the subject further by testing virgins at several ages and following the flight patterns of individual bugs for some time. Such repeated testing would also indicate how long a single bug could fly. Therefore a series of experiments was performed in which individual bugs of both sexes, virgin and non-virgin, were repeatedly flight-tested at 2- or 3-day intervals.

MATERIALS AND METHODS

The insects used for this study were descended from twenty individuals collected in October 1963 at Ann Arbor, Michigan. They were raised on a photoperiod of 16 hr. light, 8 hr. dark at a temperature of 23 ± 1°C; relative humidity was not precisely controlled, but ranged from 40–60%. Dry milkweed seeds were supplied thrice weekly with water constantly available from cotton wicks. Adults were colour-coded with spots of paint on the day following eclosion.

The method of flight-testing, by attaching a stick to the pronotum with paraffin
wax and lifting the bug from the substrate, was identical to that used previously (Dingle, 1965). In the present experiments, however, bugs were flown initially at 7 or 8 days after eclosion and thereafter flown repeatedly at 2- or 3-day intervals; previously they had been flown but once each. As before, the durations of the first five flights were used as the measure of flight activity. In some cases where an obviously long flight was taking place it was stopped after one or more hours as a matter of experimental convenience.

RESULTS

Behaviour of ‘normal’ bugs

The results of these experiments on repeated flight confirm that there is a period of maximum flight activity at the end of the teneral period. Fig. 1 shows mean flight duration, to the nearest 3-day interval, of all individuals of both sexes that flew at least once for over 30 min. Since some bugs were stopped by the experimenter (see above) the curves somewhat underestimate flight duration. They do, however, clearly indicate a flight peak at 8 days; sections taken through the cuticle showed that growth-ring deposition also ceases at that time. Bugs tested before about 6–7 days can be stimulated to no more than a few seconds of flapping flight or cannot be stimulated to fly at all. Later flights are scattered over time and show little or no tendency to be concentrated at any particular age.

Fig. 1 does not include the data for bugs which never flew more than 30 min. These ‘non-flyers’, however, represent a rather large majority, 76.2%, of the bugs tested; correspondingly only 23.8% are ‘flyers’. The behavioural differences between the two types of bug are still more evident in Table 1 which indicates that if a bug flew on its initial trial, on day 7 or 8, it was far more likely to fly at least once more on a later trial. The difference between the two groups in Table 1 is significant at $P < 0.001$. Most bugs which flew initially flew several times on later trials, so the difference between groups is conspicuous. Therefore there seem to be two distinct types of individual: those which will on some occasion fly for 30 min. or longer and those which will not.
The difference between 'flyers' and 'non-flyers' seems to be independent of sex, although there were sex differences noted. The first of these differences is that the proportion of flying females is substantially larger than the proportion of flying males—30.7% for females as opposed to 18.1% for males, calculated as above on the basis of bugs flying at least once for over 30 min. The complete data are given in Table 2 with the difference between the sexes statistically significant at $P < 0.02$. But secondly, if a male did have one of over 30 min., it was more likely than a female to have one or more further flights of similar duration. It was noted earlier that males showed two flight peaks, an initial one at 8–10 days and a second at 30–35 days (Dingle, 1965).

An equally well-defined second peak does not seem to occur in the present instance (Fig. 1), but a later period of activity in flying males is clearly indicated in Table 3. This table gives the frequency of flights of over 30 min. in males and females which are more than 20 days old and have already made such flights at 7 or 8 days. The arbitrary point of 20 days was chosen because the previous study had indicated a conspicuous diminution of flight activity at that time and hence a natural trough in the flight curve. The proportion of males making such later flights is roughly twice that of females, and the difference is significant at $P < 0.02$. Among all bugs, then, females are more likely to exhibit long flights, but among 'flyers' it is the males which are more likely to exhibit long flights repeatedly. Fig. 1 also indicates that the duration of flight in males is the longer; this was also indicated in the previous study. When bugs were allowed to fly until they stopped voluntarily, both in that case and in the present one, the longest flights were always made by males; the longest female flight was slightly over 7 hr. whereas males have flown for periods up to 13 hr. without interruption (Fig. 3).
Virgin bugs are more active than their counterparts which have been allowed to mate. Flight curves for virgin bugs flying for over 30 min. at least once, with mean duration plotted to the nearest 3-day interval, are given in Fig. 2 and should be compared with the curves for normal bugs (Fig. 1). In males the activity is revealed by the tendency for any particular flight to be longer in a virgin animal; differences were not significant statistically, but were strongly indicative. Previous comparisons using bugs tested only once (at 20 days) did show a statistically significant difference in activity between virgin and normal males (Dingle, 1965).

![Graph of Virgin Males](image1)

![Graph of Virgin Females](image2)

Fig. 2. Mean flight duration of virgin bugs as a function of age in days after the final moult. Values have been plotted to the nearest 3-day interval.

Table 4. Comparison between virgin and non-virgin females flying for over 30 min. on day 7 or 8 in respect of one or more flights of over 30 min. after day 20

<table>
<thead>
<tr>
<th>Flight after day 20</th>
<th>No flight after day 20</th>
<th>Total</th>
<th>Percentage later flights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Virgins</td>
<td>13</td>
<td>5</td>
<td>18</td>
</tr>
<tr>
<td>Non-virgins</td>
<td>8</td>
<td>16</td>
<td>24</td>
</tr>
</tbody>
</table>

The data for females were examined on the basis of the occurrence of one or more flights after 20 days in bugs initially showing a flight of 30 min. or longer at 7–8 days, as was done above in comparing the sexes (Table 3). Table 4 gives these data and indicates that virgins are indeed more likely to have a later flight than their normal counterparts; the difference between the two groups is significant at $P < 0.03$. There is no obvious inclination on the part of virgins to fly for longer periods. The heightened activity levels on the part of virgin females is thus manifested by an increased probability of long flights after 20 days. Virgins of both sexes, therefore, show an enhanced flight activity although it is exhibited in somewhat different ways.
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Individual flight capacity

With the information available on flight activity during the first 40 days of bugs' adult lives it becomes possible to estimate how far a given bug might fly in nature. Fig. 3 gives flight curves for six bugs selected to give a representative picture from all of the insects tested; there is every indication that a bug during its lifetime can remain airborne for a considerable period, if all flights are summed. For example, the virgin male in Fig. 3C flew for over 40 hr., which is undoubtedly an underestimate since on four occasions flight was stopped by the experimenter; and the virgin female in Fig. 3F flew for over 25 hr., again probably an underestimate. These bugs were virgins, which fly for longer periods, but nevertheless flights for non-virgins can still be impressive as the remainder of the graphs in Fig. 3 indicate.

Fig. 3. Plots of flight activity against time for six bugs chosen to give a representative picture of activity shown by different individuals. Dashed line above a point indicates flight was stopped by experimenter.
In order to estimate the distance bugs might cover during migration, several animals were released to fly over a measured distance to a window at one end of an otherwise darkened room. Flight speeds varied from approximately 1.5 to 2 m./sec.; taking the lower value, this represents a speed of 5.4 km./hr. In a 3 hr. flight, which is a very ordinary performance, a bug flying in a straight path as it presumably would be if migrating (Kennedy, 1961) would cover a distance of 16.2 km. Similarly, 10 hr. of flight would carry a bug 54 km., 20 hr. 108 km., or 40 hr. 216 km. Cockbain (1961) and Kennedy & Booth (1963) have noted that for aphids free flight is apt to be of shorter duration than tethered flight. But even if this is also true of Oncopeltus, a few bugs at least are probably capable of a considerable flight during their lifetimes.

The above calculations of course assume that a bug is flying in absolutely still air, a condition which in the field is virtually never met. Usually there is at least some wind. As one can readily see, a relatively gentle breeze averaging say 10 km./hr. if added to the bugs' flight speed could triple the distance travelled. At low levels many insects fly into the wind so long as it is not too strong (Kennedy, 1951), but once they have succeeded in climbing above the boundary layer (Taylor, 1958) they become wind-borne. It is therefore reasonable to assume that an individual Oncopeltus would be carried by the wind for the major portion of a long flight. Flights of 100 km. are probably fairly common, and it is likely that considerably longer excursions, possibly of 300-400 km., are by no means unusual. Under the conditions in which the bugs were raised, females do not start laying eggs until they are at least 14 days old (Dingle, 1965). Since flight begins at 7 or 8 days, they would be able to cover some distance before commencing egg deposition. From the foregoing it can thus be seen that Oncopeltus possesses considerable powers of dispersal. Since it is not listed as a 'migrant' in the literature, its powers are probably not unusual; this implies that many comparably sized insects, at the least, have similar abilities.

DISCUSSION

The peak of flight activity at 8 days, because of the duration and number of flights occurring then as well as for various other reasons, does in fact seem to represent migration in Oncopeltus (Dingle, 1965). If migration is regarded as a distinct behavioural and physiological syndrome as Kennedy (1961), Johnson (1963, 1965), and Southwood (1962) now view it, the question arises as to why relatively few, 23.8%, individuals show it. Under the conditions used in these experiments the phenomenon of long flights is obviously facultative for the species and has been shown to occur during a period of high, but not maximum, 'reproductive value' (Dingle, 1965). The behavioural polymorphism manifested as a distinction between 'flyers' and 'non-flyers' could arise primarily from genetic reasons or could be a reflexion of the environment in which the bugs were raised or both.

The first of these alternatives is based on the supposition that an individual inherits the traits of being a 'flyer' or 'non-flyer' and that these are relatively uninfluenced by the environment. If this is so, the behaviour patterns probably involve a complex of genes, for in only a few exceptional instances has it been found that only one or a few pairs of alleles determine a behaviour pattern. The second alternative, which is not wholly independent of the first, assumes that in the entire population there is a migra-
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tion tendency, but that the degree to which this is manifested is dependent on the environmental conditions. Under the least favourable conditions for flight only those bugs with the strongest tendency, presumably genetic, would be 'flyers'. Environmental factors influencing behaviour might be food, crowding (as in migratory locusts), temperature, or photoperiod. The latter is, of course, a well-known trigger of insect physiological responses, most notably diapause (Lees, 1955; Danilevskii, 1965). Many temperate-zone insects do not enter diapause under 'long-day' conditions, but do so when the photoperiod decreases to a critical length. Kennedy (1961) has pointed out that there are certain important similarities between migration and diapause, the most obvious of which is the delay of ovarian development and oviposition. Long-day conditions which accelerate reproductive development would be expected to inhibit migration at least to a certain degree (Johnson, 1965). The bugs used in the experiments reported here were raised in 16 hr. of light, which approximates to the day length of late spring and early summer in temperate regions. The low percentage of flyers may then be a result of the long photoperiod. Experiments are currently in progress (i) to try to breed a strain of 'flyers' and (ii) to attempt to change the proportion of flyers by altering photoperiod, temperature, and food level.

In nature the non-flyers would maintain a centre of dispersal in an area currently favourable for the species. The flyers would be colonizers (Dingle, 1965) to ensure the broadcasting of the species over the surrounding suitable habitats. The calculations of speed and flight capacity indicate that dispersal could take place over some distance especially if aided by wind. Oncopeltus is native over a large portion of North America, but information as to whether it overwinters in the northern parts of its range seems to be lacking. In view of its powers of flight, however, it need not overwinter in order to occupy these northern areas. There is a considerable body of evidence that several species of insect, most notably the monarch butterfly, Danaus plexippus (Urquhart, 1960) and the potato leafhopper, Empoasca fabae (Medler, 1957, 1962), do not overwinter, but move north in the spring. The latter insect, at least, is probably considerably aided by southerly winds. There is no reason why Oncopeltus could not follow a similar pattern since milkweed is available in the southern U.S. for a major portion of the winter (Brower, 1961). The earliest date that I have observed Oncopeltus in Iowa, 30 May, is consistent with recorded first observations of the potato leafhopper at the same latitude, including Iowa. Even if it does overwinter in the north, the population is undoubtedly supplemented by migrants.

In respect of sex differences, females seem to be more mobile since more of them flew for long periods. Males are more mobile when only flyers are considered, for they tended to fly longer and to fly repeatedly. Because of ovogenesis and concomitant events, it is to be expected that females are less likely to fly repeatedly; those factors promoting ovarian development would be likely to inhibit flight. That ovogenesis itself does not seem to prevent flight is indicated by the performance of virgin females. The reproductive systems of virgins do develop, and they do lay eggs (cf. also Johansson, 1958), but they are considerably more active than their counterparts which have been permitted to mate. Evidently behavioural factors, and whatever physiological responses they engender, also exert considerable influence on flight. The influence of behavioural factors is indicated in males as well, where the virgins also appear more active; in this instance gonadal development would presumably exert
far less influence. The selective advantage of emigrating from an area where mates are unavailable is obvious.

Because females carry the future of the population in the form of the eggs, they would be of greater value as colonizers than males. It is presumably for this reason that more females than males fly. In all likelihood, also, one male would be able to serve several females and so fewer would be necessary to ensure successful colonization. There has thus probably been stronger selection for migrant females than migrant males, with the result that more of the former exist in the population. In any event, when analysing insect migration the sexes cannot be lumped together, but must be analysed separately (Johnson, 1963).

**SUMMARY**

1. Individual adults of *Oncopeltus* were tested repeatedly at 2- or 3-day intervals, using tethered flight, to determine the amount of flight activity as measured by flight duration.

2. The peak period of activity occurred 8 days after the final moult with later flights scattered and showing no concentration at a particular age. Deposition of cuticular growth rings ceased at about 7 days; the peak activity was thus post-teneral and probably represents migration.

3. Only 23.8% of bugs tested showed flights of over 30 min. Those bugs which flew for long periods at 8 days were more likely to show long flights at a later age than were bugs which did not fly at day 8. There thus seems to be a behavioural polymorphism with distinct 'flyers' and 'non-flyers'.

4. More females, 30.7%, than males, 18.1%, exhibited flights of over 30 minutes. Males which did have such long flights were, however, more likely than females to have them repeatedly.

5. In both sexes virgins seemed to be more active in respect of long flights than bugs allowed continuous contact with the opposite sex.

6. Calculations based on estimates of flight speed and total duration of flight indicate that an individual migrant *Oncopeltus* is capable of covering a considerable distance, 100 kilometres or more, during its lifetime.

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**REFERENCES**


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