Acknowledgment

I thank L. H. McMullen and M. D. Atkins for critically reviewing the manuscript and D. W. Taylor and W. Kusy for assistance in the field. The temperature data were obtained through the courtesy of J. R. Marshall, Agroclimatology Sector of A.R. D.A. in British Columbia.

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SOME OBSERVATIONS ON FLIGHT IN *ONCOPELTUS FASCIATUS* (HEMIPTERA: LYGAEIDAE)[1]

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ABSTRACT

Oncopeltus fasciatus (Dallas) is a typical Hemipteran with fore-wings modified to form hemielytra and membraneous hind-wings. During flight, these two pairs of wings are linked together by a wing coupling apparatus. Observations were made on normal insects and insects with either fore- or hind-wings removed. The experiments demonstrated that the mesothorax with the fore-wings is the most important segment of the pterothorax in this insect. It was shown that the fore-wings provide the main propulsive force for flight and also provide much of the lift: the hind-wings provide extra surface for lift, but this is effective only if the wings are coupled together. As in the Lepidoptera and Hymenoptera, where the two pairs of wings are also linked together by a wing coupling apparatus, it appears that the musculature of the mesothorax may be the "driving force" for both pairs of wings.

Introduction

The Hemiptera (Heteroptera) possess two pairs of dissimilar wings; the fore-wings or hemielytra are modified and partially sclerotized, the hind-wings are thin and membranous. The two pairs of wings are normally hooked together during flight by a coupling apparatus (Weber, 1930). Comparing the Heteroptera with the Coleoptera, it might seem that the hemielytra would play little part in flight, most of the propulsion being provided by the hind-wings. However, comparison with the Lepidoptera suggests that the fore-wings might be the more important, with the hind-wings of the Heteroptera receiving their power through the wing-coupling mechanism. The studies of Scudder (1967) on flight muscle polymorphism in Notonectidae show that the mesothoracic flight muscles may be reduced in flightless members of this group, with little or no change in the metathoracic musculature. Scudder therefore suggested that the mesothoracic segment with its hemielytra is the

[1] Part of a thesis for the M.Sc. degree in the Department of Zoology, University of British Columbia, Vancouver 8, Canada.

more important segment in the flight of the Heteroptera. In the present study, experiments were carried out to test the functions and the relative importance of the two pairs of wings in the Heteroptera.

Materials and Methods

Milkweed bugs, *Oncopeltus fasciatus* (Dallas), were chosen for study because they are typical terrestrial bugs, and are easy to rear. They were fed on milkweed seeds and kept between 73°F in the dark and 78°F in the light (av. 76°F), at absolute humidity of 28%, with a photoperiod of 14 hours light and 10 dark. Under these conditions, the adults lived about two months.

Experiments were carried out to determine the relative importance of the thoracic segment in flight. Tests were made to determine the age when the adult is first able to fly, and the best age for further trials. Speed and duration tests were performed on intact insects of known age on a flight mill having a circumference of 69.10 cm. To compare the separate contributions to flight of the mesothoracic and metathoracic wings, experiments were performed in which the wings were cut off at the base and the ability to fly, and the speed and duration of free flight were tested. Only specimens which had previously flown were used in wing removal experiments. Some observations were made using a Xenon stroboscope.

Flight was initiated in untethered adults by a toss into the air, and in tethered insects, by blowing from the anterior and simultaneously removing tarsal contact (Pringle, 1957). Untethered adults were considered to exhibit true flight when they flapped their wings and moved in a more or less horizontal direction from takeoff; flight in a diagonally downward direction was also considered to be true flight but a vertical drop was not, even if the wings were flapping. For tethered adults flight was judged to occur on forward motion of the mill.

Results

Flight Period

Tests showed that the adults would not fly until three days after the last moult (Table 1).

TABLE 1. Initiation of flight in 10 **O. fasciatus** at 5 age levels.

Age in days	No. flying	Action observed
Teneral	0	none
1	0	wings extended
2	1	fluttering
3	5	flapping
4	6	flapping

It was concluded that insects used in succeeding experiments could not be less than three days old. The number of insects flying never exceeded 60% of the number tested, regardless of age. It could not be determined why apparently healthy adults resisted all efforts to initiate flight. Dingle (1965) found that eight-day-old *Oncopeltus* flew faster and longer than adults of any other age. This was confirmed in these experiments, and consequently, eight-day-old adults were used for succeeding experiments.

Normal flying insects, once flown on the flight mill, were reluctant to fly again on the mill. The reason is unknown, but was apparently not due to exhaustion. Previously tethered fliers would fly again untethered, and insects often showed mating behaviour minutes after being removed from the flight mill. Flight periods were usually from 2 to 30 minutes and rest periods between attempts ranged from 10 minutes to 24 hours.

Removal of Wings

Since not all adult insects would fly, it was necessary to test each insect untethered for a positive flight response before removing the wings. The experiments showed that the insects could fly with only the fore-wings present, but were unable to fly with the hind-wings alone. When the fore-wings were removed the hind-wings were extended but no flapping occurred. There was no difference observed in the results between males and females (Table 2).

TABLE 2. Flight response after wing removal in 8-day-old **O. fasciatus**

	Males		**Females**	
	No. oper'd on	**No. flying**	**No. oper'd on**	**No. flying**
fore-wings removed	8	0	12	0
hind-wings removed	20	16	20	17

The observation that *Oncopeltus* can fly lacking hind-wings raised the question of the necessity of these wings.

Flight duration and speed could be measured accurately only on a flight mill, and since the insects refused to fly a second time on this instrument, good values, especially for insects lacking hind-wings were difficult to obtain. Speed was measured on the flight mill in 10-sec intervals for the first 2 minutes and in 30-sec intervals after 2 minutes. It was impossible to obtain instantaneous readings for speed without sophisticated equipment, so the recorded speeds were averaged over the 10-sec or 30-sec intervals.

Both normal males and females showed an initial burst of speed, then slowed to a steady speed after 2 minutes for males and 3 minutes for females. Over the first minute, the average speeds were 63 + 3 cm/sec for males and 54 + 3 cm/sec for females. The steady speed was 57 + 2.5 cm/sec for males, and 42 + 5 cm/sec for females (Fig. 1).

From Fig 1, it appears that the best time to test flight speed is after the initial burst, while the steady speed is being maintained. This is possible for normal insects, which are

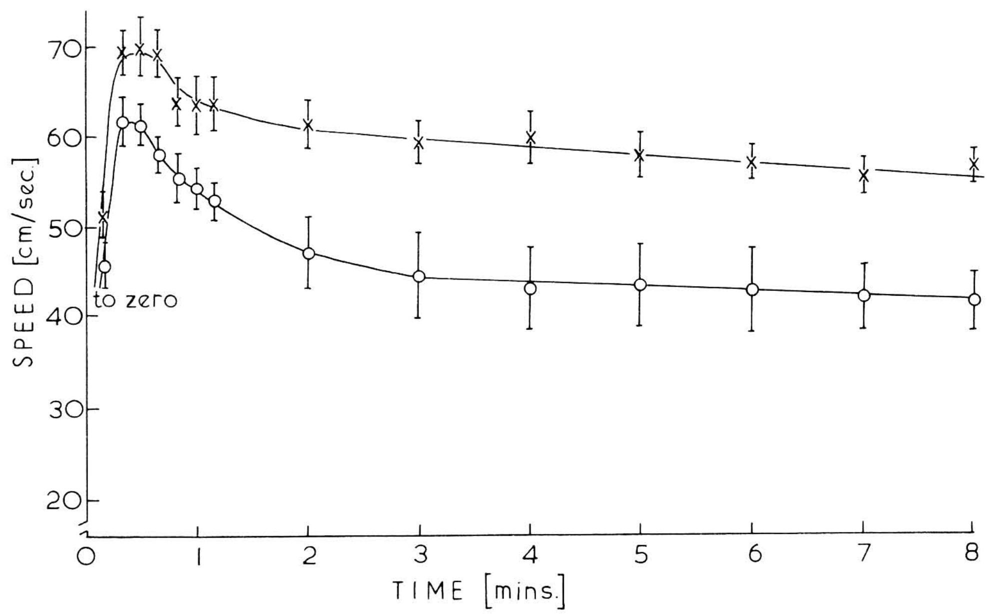

Fig. 1. Graph showing flight speed of 8-day-old **Oncopeltus fasciatus** on a flight mill: x = normal males (n = 10), 0 = normal females (n = 16) [mean ± standard error shown for each point].

able to fly for several hours if necessary (Dingle, 1965). However, the longest duration recorded on the flight mill for insects lacking hind-wings was 9 sec. Several operated insects flew in 2- to 5-sec bursts, but no sustained flight was recorded (Table 3).

TABLE 3. Duration of flight on the flight mill after removing the hind-wings in 10 male and 10 female **O. fasciatus,** 8 days old

	No. flying	Duration in sec. Av.	(range)
male	0	-	
female	4	3	(1-9)

The average speed for the few insects which flew on the flight mill following the removal of the hind-wings was computed to be 18 to 20 cm/sec, a value well below those for the normal insect (Fig. 1).

Lift was difficult to measure accurately, and so a subjective judgement was used. Four index values were assigned: 3 for insects flying diagonally upward, with lift greater than the insect's weight; 2 for insects flying directly horizontally, with lift equal to the insect's weight; 1 for insects flying diagonally downwards, with lift less than the insect's weight; and 0 for a vertical drop, with no lift present. With such numerical values, the lift could be averaged over a number of insects. The lift value was assigned after watching the insect take off and fly from the finger 2 or 3 times.

All normal insects showed lift equal to or greater than the insect's weight; those lacking hind-wings had significantly lower lift values, averaging less than the insect's weight; those lacking fore-wings showed no lift at all. Only with both pairs of wings could adequate lift be maintained (Table 4).

Wing Coupling

Experiments were performed on insects with the wing-coupling apparatus removed from the fore-wings. The results were similar to those with the insects lacking hind-wings; lift and flight speed were reduced.

In order to determine whether or not the hind-wings were moving, the insects were observed while flying illuminated solely by a stroboscope, adjusted so that the actual wing movements could be seen. Most of the insects with the wing-coupling apparatus removed refused to fly long enough for adequate observations. However, in one intact insect, flying in front of the stroboscope, the wing-coupling mechanism became disengaged about 5 minutes after flying began. After several unsuccessful attempts to reconnect the wings, the insect continued to fly, using only the fore-wings. The hind-wings did not flap on their own, but were merely held, vibrating, at an upward angle. After several minutes in this position, the hind-wings folded over the back of the insect, assuming the resting position. The fore-wings continued to flap on their own for a further 10 minutes. It is not known whether the speed was reduced during flight with the wings uncoupled, because this insect was held on a stationery tether and not on the flight mill.

Discussion

Flight requires propulsion, lift, and stability. Propulsion and lift are functions mainly of the wings and their

TABLE 4. Index values of lift for normal and operated 8-day-old **O.fasciatus**

	Normal		Lacking hind-wings	
	Number tested	Average value	Number tested	Average value
male	47	2.1	14	1.3
female	46	2.4	12	1.2

musculature; stability is a function of the shape of the wings and the body.

The experiments described show that with the hind-wings removed, *O. fasciatus* can still provide the propulsion for flight; with the fore-wings removed, propulsion is not possible. It would seem therefore that for propulsion, the mesothorax and fore-wings are more important than the metathorax and hind-wings.

It is clear that the hind-wings are necessary for adequate flight and that they provide much of the lift. Insects lacking hind-wings were unable to maintain horizontal flight and would probably not be able to take off from the ground, since the lift force provided by the fore-wings alone is less than the weight of the insect. The hind-wings are therefore important in providing the extra surface necessary to increase the lift to a value greater than that of the insect's weight. For this extra surface area to be effective, the two pairs of wings must be coupled together to present a single surface area.

It was observed, in the insect whose coupling mechanism failed, that the hind-wings did not flap unless they were coupled to the fore-wings. One is therefore led to believe that the power for movement must come from the mesothorax, transmitted to the hind wings through the fore-wings and the coupling mechanism. The hind-wings were observed to vibrate when uncoupled, indicating that the metathoracic musculature is capable of bringing about hind-wing movement. In the intact flying insect, however, the actual operation of the wings is evidently controlled from the mesothorax.

A similar situation is seen in the Lepidoptera and the Hymenoptera in which the two pairs of wings are also joined by coupling mechanisms, and the power for flight comes from the mesothorax. For adequate lift and propulsion, both pairs of wings are necessary, but both are controlled by the mesothoracic musculature, acting through the hook mechanism and through the metathoracic muscles in some cases (Chadwick, 1953; Pringle, 1968).

In the Heteroptera it would thus seem that the mesothoracic segment is the most important part of the pterothorax for flight. The modification of the fore-wings to form hemielytra has not progressed so far that it has reduced the functional siginificance of the mesothorax to the stage seen in the Coleoptera.

Acknowledgments

The research for this paper was supported by a grant from the National Research Council of Canada to Dr. G. G. E. Scudder.

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